Vol. 90. Part 4. Pp. 63-105, 12 figs. 15th June, 1940

INST. ENT.
LIBRARY
10 JUN 1940
Ex. 344

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGE

JAYEWICKREME, S. H., Ph.D. A comparative study of the larval morphology of leaf-mining Lepidoptera in Britain . . . 63–105, 12 figs.

LONDON:

PUBLISHED BY THE SOCIETY AND

SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 12s. 0d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION, 1940–1941.

K. G. Blair, D.Sc., *President.*

G. Fox-Wilson.
J. C. F. Fryer, O.B.E., M.A. } *Vice-Presidents.*
N. D. Riley.

N. D. Riley, *Treasurer.*

O. W. Richards, M.A., D.Sc., *Secretary.*

F. J. Griffin, A.L.A., *Registrar.*

Other Members of Council.

E. A. Cockayne, M.A., M.D., F.R.C.P.
C. N. Hawkins.
Col. F. A. Labouchere.
Hugh Main, B.Sc.
Sir Guy A. K. Marshall, C.M.G., D.Sc., F.R.S.
A. M. Massee, D.Sc.
The Hon. Miriam Rothschild.
J. Smart, B.Sc., Ph.D.
W. R. Thompson, Ph.D., D.Sc., F.R.S.
B. P. Uvarov, D.Sc.
A. Welti.
V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S.

Finance and House Committee.

A. Welti (Chairman).

Brig.-Gen. B. H. Cooke, C.M.G., C.B.E., D.S.O.
C. N. Hawkins.
Francis Hemming, C.M.G., C.B.E.
R. W. Lloyd.
J. Smart, B.Sc., Ph.D.

Publication Committee.

V. B. Wigglesworth, M.A., B.Ch., M.D., F.R.S. (Chairman).

E. A. Cockayne, M.A., M.D., F.R.C.P.
G. Fox-Wilson.
A. M. Massee, D.Sc.
Hugh Scott, M.A., Sc.D.
W. R. Thompson, Ph.D., D.Sc., F.R.S.

Library Committee.

B. P. Uvarov, D.Sc. (Chairman).

E. B. Britton.
B. M. Hobby, M.A., D.Phil.
R. W. Lloyd.
W. H. T. Tams.
W. R. Thompson, Ph.D., D.Sc., F.R.S.

Committee for the Protection of British Insects.

W. G. Sheldon (Chairman).

Capt. E. Bagwell-Purefoy.
C. L. Collenette.
W. J. Dow.
J. C. F. Fryer, O.B.E., M.A.
Col. F. A. Labouchere.
N. D. Riley.
H. M. Edelsten (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Sir Guy A. K. Marshall, C.M.G., D.Sc., F.R.S., appointed 1939.
   Dr. Karl Jordan, F.R.S., appointed 1936.
2. **Conference of Delegates of Corresponding Societies of the British Association for the Advancement of Science.**
   Mr. H. B. Cott, M.A., appointed 1939.
3. **International Congress of Entomology** (Berlin 1938).
   J. C. F. Fryer, O.B.E., M.A. *Francis Hemming, C.M.G., C.B.E.*
   A. D. Imms, M.A., Sc.D., F.R.S.
4. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten. *Mr. E. C. Bedwell.*
   [Delegates nominated by Committee for the Protection of British Insects.]
5. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. W. G. Sheldon, appointed 1922.
6. **New Forest Association.**
   Mr. W. Fassnidge, appointed 1934.
7. **Royal Meteorological Society. Phenological Committee.**
   Dr. C. B. Williams, appointed 1937.

A COMPARATIVE STUDY OF THE LARVAL MORPHOLOGY OF LEAF-MINING LEPIDOPTERA IN BRITAIN

By S. H. Jayewickreme, Ph.D.

Manuscript received 21.iv.1939.

(Read 7th February, 1940.)

Contents.

		PAGE
I.	Introduction	63
II.	Material and methods	64
III.	General descriptions of leaf-mining larvae	
	Gelechiidae	65
	Cosmopterygidae	70
	Plutellidae	70
	Coleophoridae	71
	Lamproniidae	71
	Gracilariidae	72
	Lyonetiidae	80
	Tischeriidae	85
	Nepticulidae	87
	Eriocraniidae	89
IV.	Discussion	90
V.	The leaf-mining habit in relation to the phylogeny of the Micro-lepidoptera	97
VI.	Summary	103
VII.	References	104
VIII.	List of abbreviations used	105
IX.	Index to species described	105

I. Introduction.

Although the biology of leaf-mining Lepidoptera has exercised the curiosity of entomologists since De Geer first described the habits of the larva of *Nepticula anomalella* Gz. in 1737 (see Needham, Frost and Tothill, 1928), the morphology of the larvae has been a comparatively neglected study. The earliest work on these lines was that of Chambers (1879), who described the " Flat-Larval " or *cameraria* group of *Lithocolletis*. His work from a morphological standpoint is now only of historic interest and this rather extraordinary group of leaf-mining larvae, occurring only in North America, has still to be dealt with satisfactorily. The work of Braun (1909) in this direction throws some light on the matter, but even her descriptions are not sufficiently detailed.

The Gracilariidae are peculiar in going through a hypermetamorphosis, in which the larva is a sap-feeder in the earlier stages. Chapman (1902), who attempted a classification of *Gracilaria* and allied genera, never realised the significance of this stage in the life history, nor did Braun and other previous workers. Trägårdh (1913) first showed that these larvae were perfectly adapted for obtaining such sustenance, and his work, which will be referred to often in this paper, was the first attempt to study the adaptations of lepidopterous

larvae to the leaf-mining habit. One criticism that must be levelled against his fine work is that he considered the very specialised genera he studied as typical of leaf-mining larvae as a whole. That his assumption was erroneous will be apparent in the ensuing pages.

The highly specialised leaf-mining genus *Opostega*, unrepresented by leaf-mining species in Britain, has been described by Heinrich (1918). Grandi (1933) has recently described in great detail a large number of species of leaf-mining larvae. These accounts have proved useful in the present study. It is, however, unfortunate that Grandi does not usually figure the larval hypopharynx.

The object of the present study has been to examine a large number of leaf-mining genera and species with a view to a more complete understanding of the leaf-mining habit. Thus, thirty species belonging to seventeen genera have been examined in addition to seven genera described by Trägårdh (1913), Busck and Böving (1914), Heinrich (1918) and Grandi (1933), and it may be asserted that no really important genus has been overlooked.

This work was carried out in the Department of Zoology and Applied Entomology of the Imperial College of Science and Technology, London, under the direction of Professor J. W. Munro, to whom I am indebted. My thanks are due to Dr. O. W. Richards for advice and criticism.

II. Material and Methods.

The larvae, which were mainly collected at the Imperial College Biological Field Station, Slough, were identified with the aid of Meyrick, 1928, *Handbook of British Lepidoptera*, Hering, 1935–37, *Die Blatt-Minen Mittel- und Nord-Europas*, and Tutt, 1899, *British Lepidoptera*. It was generally found possible to identify the larvae by such characteristics as colour, colour or markings of thorax, abdomen, etc., in conjunction with features of the mine itself, which is usually very specific. These identifications were checked in the majority of instances by breeding the adults.

Preparations of the mouth-parts were made by first dissecting them and then boiling in a weak solution of KOH. They were then usually stained in Carbol Fuchsin and mounted in the usual manner, in cavity slides when necessary. Whole mounts of larvae were made by dehydrating them very gradually in alcohol, clearing in clove oil and mounting them in cavity slides. A modified form of Berlese's Fluid was also used with success.

III. General Descriptions of Leaf-mining Larvae.

The following descriptions have mainly a comparative rather than a strictly taxonomic view-point, and are thus not meant to be exhaustive. The aim has been to stress modifications due to the leaf-mining habit. In general, a structure will be described and, if necessary, discussed in connection with the first species in which it is met. In the succeeding species it will only be mentioned briefly. To avoid duplication of description reference is made in a number of instances to the work of Trägårdh (1913). These structures are, however, illustrated in this paper from original preparations.

The descriptions of those species that mine for a part of their larval lives applies to the mining stages only.

The ocelli are described according to the following description of Fracker (1915) : " The dorsal four ocelli usually form the quadrant of a circle, with the other two below them and further apart. Beginning at the caudal ocellus of

the dorsal group we may call them the first to fourth in regular order. The fifth is caudo-ventral of the fourth and in some cases further ventrad than the sixth which is the most cephalic in position."

In the descriptions of the labrum the terms epipharyngeal shield, epipharyngeal setae and epipharyngeal cuticular spines have been retained because of their common usage. An epipharynx as such is not present in lepidopterous larvae.

To facilitate description of the mandibles an arbitrary system of numbering the teeth has been adopted. Thus, the tooth nearest the mesal edge is referred to as the first, the next to it the second and so on.

The arrangement of the crotchets on the abdominal legs has been described after Fracker.

The arrangement of the body setae and the structure of the spiracles have not been dealt with in the present study.

Gelechiidae.

Aristotelia hermanella (Fabr.).

The larva, which has an unflattened or cylindrical body, mines throughout life a gallery which is very narrow at its commencement. In later instars the mine appears to be a blotch which is due to the larval habit of repeatedly cutting across the gallery already made.

The head capsule (fig. 1, a, b), which is unflattened, is characterised by a pair of posterior, triangular, dorsal prolongations which extend half-way into the prothorax. They extend far beyond the limit of the ventral surface of the head. The clypeus (fig. 1, a; CL) is a prominent dorsal triangular plate with its margins defined internally by a strong V-shaped ridge, the epistomal ridge (ER), the inverted apex of which is continuous with the thick median ridge of the dorsal wall of the cranium, which in turn represents the inflected frons (F). The anterior edge of the clypeus is strengthened by an internal submarginal thickening (SMR), forming a bracing ridge between the dorsal articulations of the mandibles (the anterior articulations of external feeding hypognathous forms).

Ventrally, on each side there is a triangular hypostomal area (fig. 1, b; H), which is a posterior median extension of the postgena (PG) and is separated from it by the hypostomal suture, marked internally by a well-developed ridge, the hypostomal ridge (HR). The hypostomal areas do not quite meet in the median line.

A narrow subgenal ridge (fig. 1, a, b; SGR) follows the outer margins of the membranous area of the antennal base from the dorsal to the ventral articulation of the mandible, and is then continued along the anterior margin of the hypostoma. The hypostomal ridge is strongly developed and runs from the subgenal ridge at the ventral mandibular articulation to the postoccipital ridge (fig. 1, b; VA). Its function appears to be to brace the genal area between the mandible and the posterior rim of the head. The postoccipital ridge is characterised by the presence of a pair of well-developed dorsal apodemes (fig. 1, a, b; DA) and a pair of ventral apodemes (fig. 1, b; VA) which are less well developed. To these apodemes are attached the anterior ends of the prothoracic muscles.

The tentorium consists of an anterior pair of well-developed bars, the anterior tentorial arms (fig. 1, a, b; AT), which arise on the lateral parts of the epistomal

ridge about midway. They extend horizontally through the head and are united posteriorly with the ends of the tentorial bridge (TB) which consists of two parts, the posterior tentorial arms (PT) and the tentorial bridge proper. The posterior tentorial arms have their origin on the posterior angles of the hypostomal areas. The morphology of these structures has been worked out mainly from the studies of Snodgrass (1928).

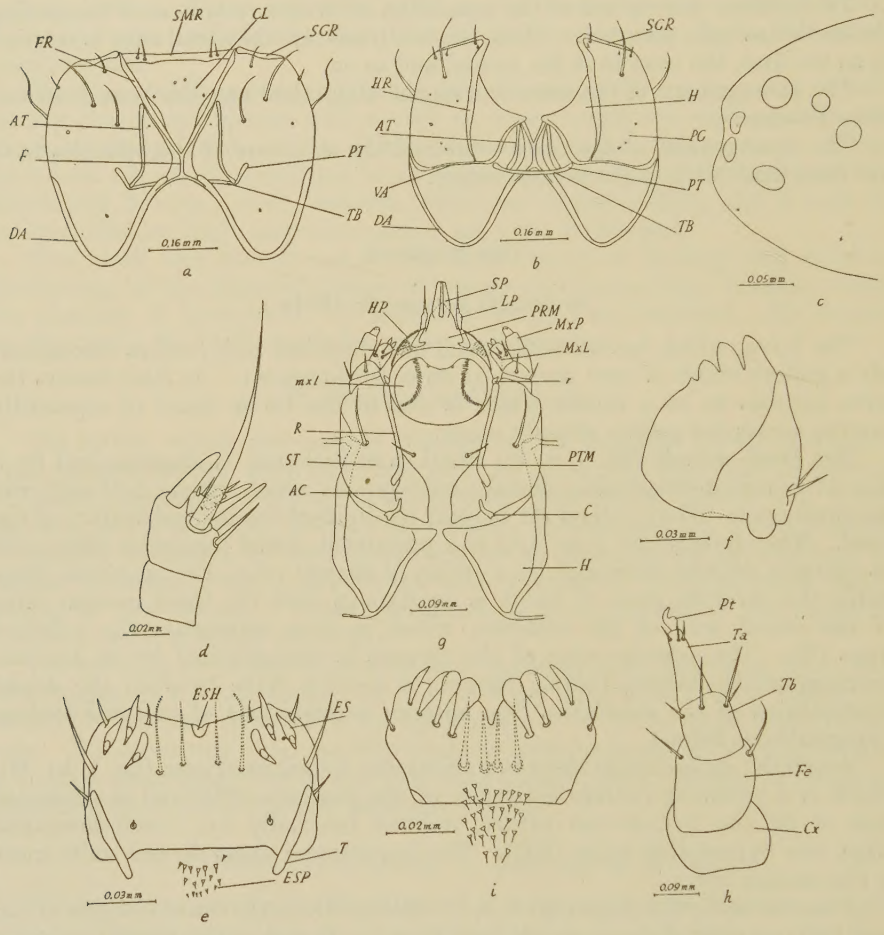


FIG. 1.—*Aristotelia hermanella* (Fabr.). a, head, dorsal view; b, head, ventral view; c, ocelli of left side; d, left antenna, ventral view; e, labrum, ventral view; f, left mandible, ventral view; g, underlip, ventral view; h, left mesothoracic leg (late stage), ventral view. *A. stipella* Hb. i, labrum, ventral view.

The head capsule of *A. hermanella* may be regarded as being typical of the unflattened head. In future only salient points will be mentioned, where it is necessary to bring out the difference between specialised heads and the general pattern as exemplified by *A. hermanella*. It will be referred to as the *Aristotelia* type.

There are six ocelli (fig. 1, c), of which the first, second and third are dorsal

and the fourth is marginal and placed immediately posterior to the antenna. The sixth ocellus is ventral and lies below the fourth, while the fifth, also ventral, lies below the third. There is a wide gap between the first and fifth ocelli.

The antenna (fig. 1, d) is situated in the membranous area lying between the dorsal and ventral articulations of the mandible (the anterior and posterior of external feeding hypognathous forms). As this position of the antenna holds good for all forms it will not be repeated again. There are three segments, of which the second is the largest. The basal segment, which is about two-thirds the size of the second, is devoid of sensorial papillae and setae. The second segment carries two long, narrow, conical sensorial papillae, a moderately long seta and one very long seta, which is about twice the length of the antenna itself and curved inwards. All these structures are placed at the distal end of the segment. The third segment is very small and carries two conical sensorial papillae, one of which is about four times the size of the other, a small seta and a rectangular protuberance carrying a bristle at its apex. As the basal segment, when present, never carries any sensorial papillae nor setae in any species this point, too, will not be repeated again. The majority of species examined have an antenna similar to that of *A. hermanella*, which will be referred to as the *Aristotelia* type.

The labrum (fig. 1, e) is a broad, rectangular, flat plate. Its anterior margin is slightly concave with a very small median incision. A small sclerotised area round this incision is the epipharyngeal shield (ESH). There are two pairs of dorsal and five pairs of ventral setae. The three pairs of ventral epipharyngeal setae (ES) are well developed and the middle pair projects forwards beyond the anterior edge of the labrum. The epipharyngeal cuticular spines (ESP) are very few in number and are not present on the ventral surface of the labrum itself. Tormae (T), sclerotised rods on which the labial muscles are inserted, are present at the postero-lateral angles.

The mandible (fig. 1, f) has five teeth, of which four lie dorsally. These latter teeth lie on the same level owing to the flattening of that part of the mandible carrying them. The fifth or ventral tooth is smaller than the preceding one. The hinge line connecting the dorsal and ventral articulations is oblique and proceeds downwards and inwards. In the descriptions that follow, this point, in which the majority of larvae agree, will not be repeated, but any divergence will be noted.

The large, projecting underlip is composed of the united maxillae, labium and hypopharynx and is supported basally on the mesally approximated hypostomal areas (fig. 1, g; H) of the postgenae, which in lepidopterous larvae have separated the labium from its basal connection with the neck membrane. The maxillae are large lateral lobes and each consists of a small, bent, proximal sclerite, the cardo (C), articulating with the anterior margin of the hypostomal area. The stipes (ST) forms the most conspicuous part of the maxilla and is characterised by a very strongly developed ridge (R) running along the mesal margin, on which the stipital muscles are inserted. Distally each stipes ends in a lobe consisting of a four-segmented maxillary palpus (MXP) with a smaller mesal lobe, the maxillary lobe, given off from its second segment, which has two apical sensory papillae. For a discussion on the homology of the maxillary palpus and lobe see Das (1937).

The labium lies between the laterally placed maxillae, and consists of a proximal and largely membranous postmental region (PTM) and a distal prementa region (PRM). The former has two sclerites (AC) at its postero-lateral angles, the homology of which is uncertain and has been discussed by

Das. The prementum (PRM) forms a free, projecting anterior median lobe with the hypopharynx (HP) lying adnate upon its anterior surface. The spinneret (SP), which in early stages is rather ill developed, is borne at the distal extremity of the lobe and carries the opening of the silk duct at its tip. A pair of two-segmented labial palpi (LP) is present on either side of it. This spinneret-bearing lobe is supported laterally on the distal arms of the mesal ridges of the maxillary stipites. A pair of small sclerites (r) act as fulcra, and on these the entire spinning apparatus can be swung in and out, carrying with it the hypopharynx.

The hypopharynx which lies dorsally and is attached to the premental lobe is covered with hairs anteriorly and has two lateral, hairy lobes (mxl) which have been called maxillulae by De Gryse (1915), superlinguae by Folsom (1909) and paraglossae by older authors.

Many species have an underlip similar to that of *A. hermanella* and descriptions of these on the above lines would be mere repetition. Therefore, only salient points will in future be mentioned and the underlip of *A. hermanella* will be referred to as the *Aristotelia* type.

In the first instar the thoracic legs are minute and four-segmented. In later instars they are well developed and consist of four segments (the trochanter being very difficult to make out), a basal coxa (fig. 1, h; Cx), femur (Fe), tibia (Tb), tarsus (Ta) and the pretarsus or claw (Pt). This well-developed thoracic leg will be referred to as the *Aristotelia* type.

Abdominal legs are present on segments three to six. In the first instar there are no abdominal legs or crotchets. In the second long, slender prolegs appear with no crotchets. In the third and fourth instars crotchets are present on the mesal surface.

The anal legs are small with no crotchets.

Aristotelia stipella Hb.

The larva, which has a cylindrical body, mines a whitish blotch in the leaves of *Chenopodium*. It differs from *A. hermanella* only in the structure of the labrum (fig. 1, i), which is rather modified, and has a moderately deep median incision. Ventrally, two pairs of epipharyngeal setae are developed into large, club-shaped structures, while a third pair of ordinary setae are large and blade-like. These four pairs of setae project forwards beyond the anterior edge. Only about ten moderately long epipharyngeal spines are present at the base of the labrum.

Recurvaria nanella Hb.

The larva has a cylindrical body and mines for three instars a narrow open gallery with short side branches. It consumes all the tissue between the upper and lower cuticles and lines both roof and floor of the mine with silk.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

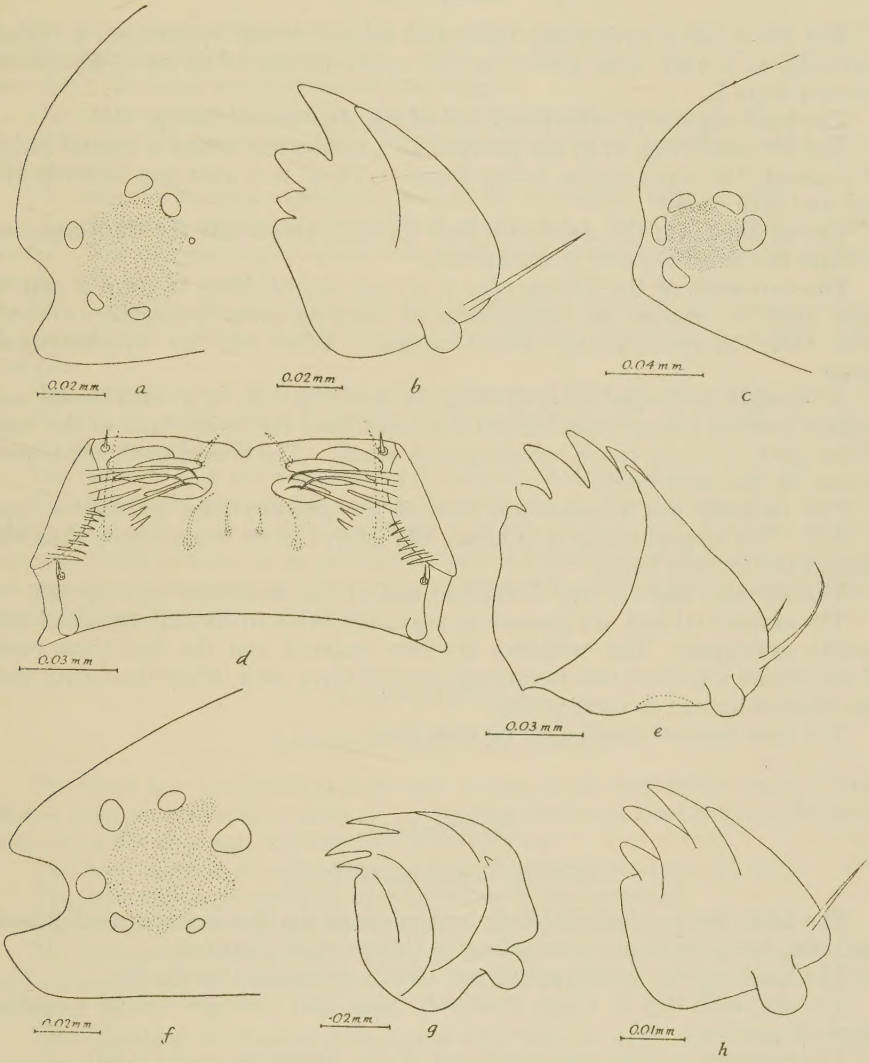
The six ocelli (fig. 2, a) are arranged round a central patch of pigment, but the first ocellus is very small and rudimentary.

The antenna is three-segmented and of the *Aristotelia* type (p. 67).

The labrum is deeply bilobed but unmodified, with a broad patch of epipharyngeal spines.

The mandible (fig. 2, b) has five teeth, of which the first four lie dorsal and are placed almost on the same level. The fifth, most ventral, tooth is smaller than the fourth.

The underlip is of the free-swinging *Aristotelia* type (p. 67) with the spinneret well developed at all stages adapted to the larval habit of lining the gallery with silk.



2

Fig. 2.—*Recurvaria nanella* Hb. a, ocelli of left side; b, left mandible, ventral view. *Mompha* sp. c, ocelli of left side; d, labrum, ventral view; e, left mandible, ventral view. *Plutella maculipennis* Curt. f, ocelli of left side; g, left mandible, ventral view. *Coleophora nigricella* Steph. h, left mandible, ventral view.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are present on segments three to six and have a weakly developed uniserial circle of small, uniordinal crotchets.

The anal legs are small with a well-developed row of crotchets anteriorly.

Cosmopterygidae.

Mompha sp.

The larva has a cylindrical body and mines, venter uppermost, a blotch beginning as a long, open gallery on the upper surface of leaves of *Epilobium angustifolium* L.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

The five ocelli (fig. 2, c) are grouped in a semi-circle round a central patch of pigment, the sixth ocellus being absent. There is a wide gap between the first and fifth ocelli.

The antenna is of the *Aristotelia* type (p. 67), except that the third segment is about one-third the size of the second.

The two sides of the labrum (fig. 2, d) are turned down to form a pair of flaps, with a number of outgrowths of varying sizes projecting inwards from their morphologically dorsal surface. There are no epipharyngeal spines.

A strongly developed ridge divides the mandible (fig. 2, e) into dorsal and ventral areas of almost equal extent and runs from the mesal base to the base of the sixth, ventral, tooth, which is very small. The dorsal teeth are placed almost on the same level.

The underlip has a premental lobe of the free-swinging *Aristotelia* type (p. 67). The hypopharynx is trilobed, the lateral lobes being larger than the median and densely hairy.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are present on segments three to six and are small and weakly developed. The crotchets are very reduced and the first three pairs of abdominal legs have two transverse rows of three each, while the fourth pair has three crotchets on each proleg.

The anal legs are small with no crotchets.

Plutellidae.

Plutella maculipennis Curt.

The larva has a cylindrical body and mines in the first instar a small blotch beginning as a very short open gallery in the leaves of *Brassica*.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

The six ocelli (fig. 2, f) are relatively large and arranged round a central patch of pigment.

The antenna is three-segmented and of the *Aristotelia* type (p. 67).

The labrum is unmodified.

The mandible (fig. 2, g) has a strongly convex outer margin on which are placed five very sharp teeth, all on different levels, of which the most ventral is vestigial.

The underlip has a premental lobe of the free-swinging *Aristotelia* type (p. 67). The hypopharynx is trilobed and hairy at the apex.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are present on segments three to six, are long and slender and set on broad bases. They have a well-developed uniserial circle of uniordinal crotchets.

Coleophoridae.

Coleophora nigricella Steph.

The larva has a cylindrical body and mines, only in the first instar, a small blotch beginning as a short gallery. After the first moult the larva cuts out a case from the mine and becomes a case-bearer.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

There are five ocelli, the sixth being absent, grouped round a central patch of pigment.

The antenna is three-segmented and of the *Aristotelia* type (p. 67).

The labrum is relatively unmodified except for a very large epipharyngeal shield. The epipharyngeal spines are moderately long and extend as a broad patch back to the mouth.

The mandible (fig. 2, h) has five teeth, of which the first two are placed on the same level but the third, fourth and fifth are placed on a curved outer margin.

The underlip has a free-swinging premental lobe of the *Aristotelia* type (p. 67), but the spinneret is ill developed in the first instar. It attains its normal size in the second instar.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

No abdominal legs are present in the first instar and the anal legs are provided with only four or five crotchets. In the second instar, which is case-bearing, three or four small crotchets mark the position of the abdominal legs on segments three, four and five only. The anal legs are well developed with a semi-circle of crotchets anteriorly.

Lamproniidae.

Incurvaria muscalella (Fabr.).

The larva has a cylindrical body and mines, in the first instar only, a small blotch beginning as a short gallery. After the first moult in the mine the larva cuts out a flat case and is thereafter a case-bearer.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

The six ocelli show nothing unusual in their arrangement.

The antenna is three-segmented and of the *Aristotelia* type (p. 67).

The labrum is unmodified. The epipharyngeal spines are moderately long and proceed back to the mouth in two strands beginning at the middle of the labrum.

The mandible is divided into dorsal and ventral areas by a strong ridge running from the mesal base to between the second and third teeth. The first two teeth are placed on the same level, while the other three are placed on a gradually convex outer margin. The fifth, most ventral, tooth is smaller than the fourth.

The underlip has a premental lobe of the free-swinging *Aristotelia* type (p. 67), but the spinneret is ill developed in the first instar. It attains its normal size in the second instar.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are marked by the presence of crotchets on segments three to six and consist of a transverse band of uniordinal crotchets.

The anal legs are small with no crotchets.

Gracilariidae.

The larvae belonging to this family are peculiar in going through a hypermetamorphosis. For two or more instars they are sap-feeding and then revert to the normal tissue-feeding type.

Lithocolletis concomitella Bankes.

The sap-feeding larva has a very flattened body and mines for three instars a blotch in the lower epidermis of apple leaves.

The wedge-shaped head (fig. 3, a) is very flattened with the posterior dorsal prolongations moderately well developed. The two arms of the epistomal ridge (ER) run parallel for most of the way but diverge slightly at the posterior end and are then connected by a slender, arched, transverse bar (ptb). They then become continuous with the dorsal apodemes (DA) of the postoccipital ridge, which are strongly developed. A short transverse ridge (TR) proceeds dorsally inwards from the lateral margin of the posterior extremity of the head, somewhat posterior to the transverse bar connecting the two arms of the epistomal ridge. The hypostomal areas (H) are moderately well developed and not separated to quite such an extent as in other sap-feeding larvae.

Four heavily pigmented ocelli (fig. 3, f; *L. coryli* Nic.) are placed one behind the other on or about the margin, the first being just posterior to the antenna.

The antenna (fig. 3, b), labrum (fig. 3, f; *L. coryli* Nic.), mandible (fig. 3, c) and underlip (fig. 3, d) are all specialised and have been described by Trägårdh.

No thoracic, abdominal or anal legs are present, but in the third instar three pairs of minute protuberances appear on the thoracic segments and a pair on each of the abdominal segments three to five.

From the fourth instar onwards (there are six in all) the larva reverts to the normal tissue-feeding habit and has a cylindrical body. It proceeds to spin silk on the underside of the cuticle of the mine, which on hardening contracts, thus raising the roof of the blotch and giving rise to a so-called " tentiform " mine.

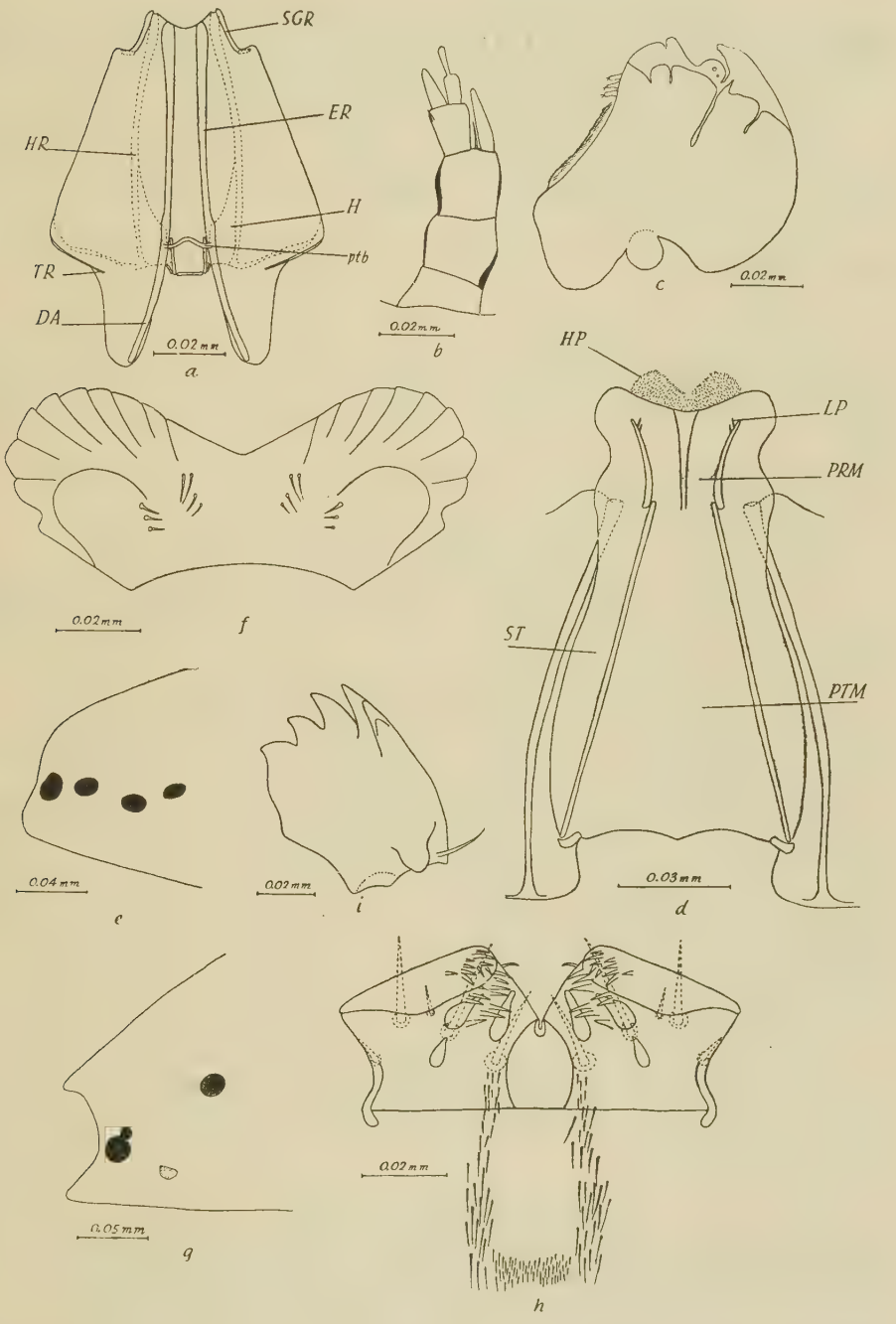
The head capsule is unflattened and of the *Aristotelia* type (p. 66), but as the larva is semi-prognathous it is held at an angle of about 45° to the long axis of the body.

There are four ocelli (fig. 3, g), two of which are contiguous and placed submarginally behind the antenna. Another is placed dorsally some distance away, while a fourth lies ventral and nearer to the anterior group. All the ocelli are pigmented, the anterior group being especially so.

The antenna is three-segmented and of the *Aristotelia* type (p. 67), except that the basal segment is slightly larger than the second while the third segment is also relatively larger.

The labrum (fig. 3, h) is deeply bilobed with a shallow median incision anteriorly. Its antero-lateral margins are turned down ventrally to form a flap with several stout, hair-like outgrowths present on its morphological dorsal surface and pointing ventralwards. Further outgrowths are present on the anterior ventral surface, which are continuous with the long epipharyngeal spines leading back to the mouth.

The mandible (fig. 3, i) is rather flattened dorsally and has six teeth, of which the fourth, fifth and sixth are slightly more ventral than the rest which are placed on the same level. The three dorsal teeth are larger than the ventral, while the sixth, which lies at the base of the fifth, is vestigial.



3

FIG. 3.—Sap-feeding stage of *Lithocolletis concomitella* Bankes. a, head, dorsal view; b, left antenna, ventral view; c, left mandible, ventral view; d, underlip, ventral view. Sap-feeding stage of *L. coryli* Nic. e, ocelli of left side; f, labrum, ventral view. Tissue-feeding stage of *L. concomitella* Bankes. g, ocelli of left side; h, labrum, ventral view; i, left mandible, ventral view.

The underlip is of the *Aristotelia* type (p. 67) with a free-swinging premental lobe. The hypopharynx is trilobed and very hairy especially at the apex, while the median lobe is much larger than the lateral lobes.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

Abdominal legs are present on segments three, four, and five only. They are well developed and have almost two complete circles of strong uniordinal crotchets, the inner being composed of slightly larger hooks. This is a reduced multiserial arrangement.

The anal legs are well developed with a semi-circle of well-developed crotchets anteriorly.

Acrocercops brongniardella (Fabr.).

The sap-feeding larva was not available. Several larvae mine whitish galleries on the upper surface of leaves of oak, which in the tissue-feeding stage coalesce to form a large blotch, often occupying the entire upper surface of the leaf.

The sap-feeding larva of *A. strigifinitella* Clemens has been described by Heinrich and De Gryse (1915).

The tissue-feeding larva of *A. brongniardella* has a cylindrical body.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

There are six ocelli (fig. 4, a) placed in two groups, an anterior and a posterior. The former has three ocelli, the third, fourth and sixth, while the latter is composed of the large first and second ocelli. The fifth ocellus is very large and occupies an intermediate position.

The antenna is three-segmented and of the *Aristotelia* type (p. 67).

The labrum is relatively unmodified but shows a remarkable development of the epipharyngeal spines which cover almost the entire ventral surface and extend backwards to the mouth as a broad patch.

The mandible (fig. 4, b), which has six teeth, is triangular in shape and has a broad and massive base. A well-marked ridge running from the region of the mesal base to the base of the fifth tooth demarcates dorsal and ventral areas. The first three teeth are placed on the same level but from that point the external margin becomes gradually convex. The fifth and sixth teeth are ventral, the latter being very small.

The underlip has a premental lobe of the free-swinging *Aristotelia* type (p. 67). The hypopharynx has a pair of bilobed maxillulae which are very hairy, the hairs pointing backwards.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are present on segments three, four and five only and have a uniserial circle of well-developed uniordinal crotchets.

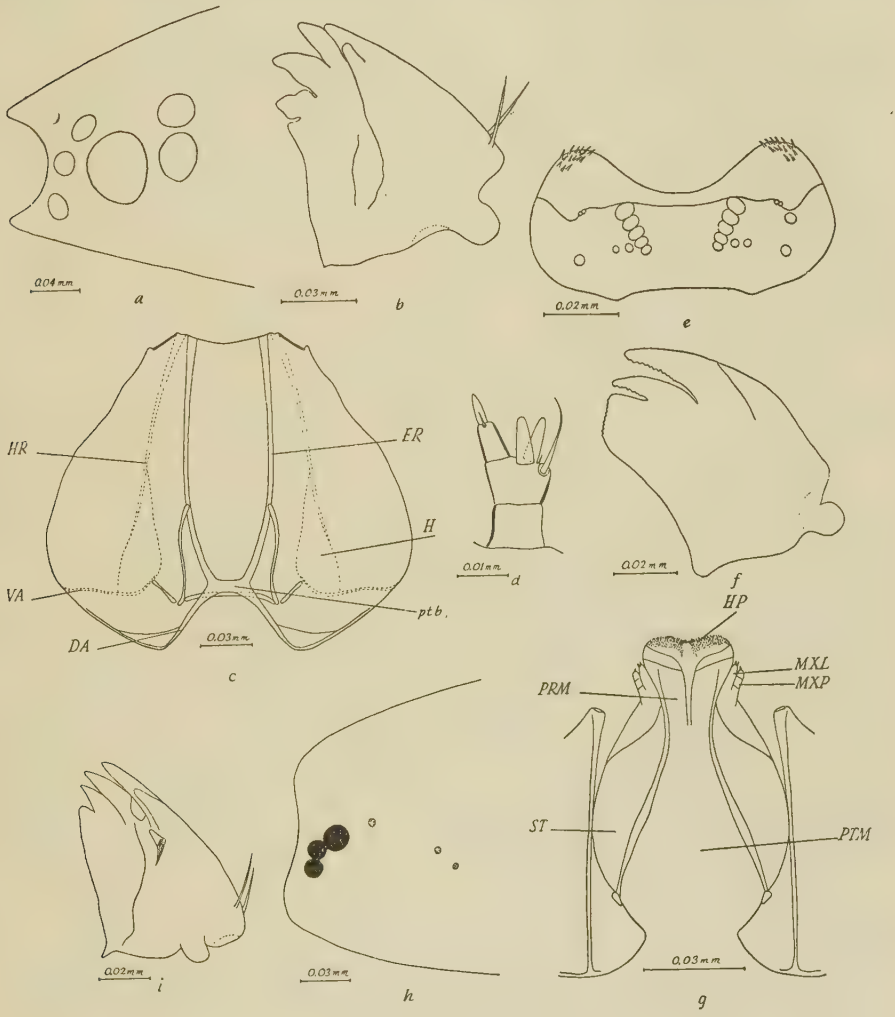
The anal legs are well developed with a semi-circle of well-developed crotchets anteriorly.

Parectopa syringella (Fabr.).

The sap-feeding larva has a very flattened body. Several larvae mine, side by side, a common blotch beginning as separate, short galleries which soon coalesce, on the upper surface of leaves of *Syringa* and *Ligustrum*.

The head capsule (fig. 4, c) is very flattened and wedge-shaped. The posterior dorsal prolongations are rather small and pass into the anterior region of the prothorax. The dorsal apodemes (DA) of the postoccipital ridge are better developed than the ventral (VA). The two arms of the epistomal ridge (ER) run parallel for about two-thirds of the way and then converge

slightly to be connected at their posterior ends by a short, broad transverse bar (ptb). The hypostomal areas (H) are small and triangular in shape and are widely separated, while the hypostomal ridges (HR) diverge slightly. The



4

FIG. 4.—Tissue-feeding stage of *Acrocercops brongniardella* (Fabr.). a, ocelli of left side; b, left mandible, ventral view. Sap-feeding stage of *Parectopa syringella* (Fabr.). c, head, dorsal view; d, left antenna, ventral view; e, labrum, ventral view; f, left mandible, ventral view; g, underlip, ventral view. Tissue-feeding stage of *P. syringella* (Fabr.). h, ocelli of left side; i, left mandible, ventral view.

subgenal ridges (SGR) are very weakly developed. Dimmock (1880) has described the head of this species very inaccurately.

Four ocelli, in two groups of two each, are placed marginally at the

posterior extremity of the head. The anterior pair is densely pigmented and the posterior faintly so.

The antenna (fig. 4, d) is relatively small and consists of three segments. The second segment has two conical sensorial papillae, two small setae and the "long" seta found in *Aristotelia* is here relatively short and curved inwards. The third segment carries a single conical sensorial papilla and a seta. Trägårdh says that this species has only two segments, which is at variance with my observations.

The labrum (fig. 4, e) is specialised and has been described by Trägårdh.

Four teeth are present in the mandible (fig. 4, f) of which the tooth nearest to and continuous with the mesal edge is enormously developed, conical and slightly serrate. A fourth tooth lies external to and fused with the third. The hinge line connecting the dorsal and ventral articulations proceeds directly downwards.

The underlip (fig. 4, g) is very specialised and has been described by Trägårdh. Dimmock correctly described the maxillae but mistook the hypopharynx for the labium.

No thoracic, abdominal or anal legs are present.

The tissue-feeding stage of *P. syringella* has a cylindrical body and mines in the leaf in the third instar. It then quits the mine to become a leaf-roller.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

The fourth, fifth and sixth ocelli (fig. 4, h) form an anterior, pigmented group and are relatively large and contiguous. The first, second and third ocelli are much smaller, there being a wide gap between the second and third. These ocelli are not pigmented to quite such an extent as the others.

The antenna is three-segmented and of the *Aristotelia* type (p. 67).

The labrum is deeply bilobed with a small median incision anteriorly and has small hair-like outgrowths, some of which project forwards from the anterior margin. They become continuous with the epipharyngeal spines, which are numerous, moderately long and extend backwards as a broad patch.

The mandible (fig. 4, i) is divided into dorsal and ventral areas by an oblique ridge running from the mesal base to the base of the third tooth. There are seven teeth placed on a convex outer margin, of which the fourth has a small, vestigial, rectangular tooth lying alongside it. The fifth also has at its base a small vestigial tooth. This description is at variance with that of Trägårdh, who describes only five teeth.

The underlip is of the *Aristotelia* type (p. 67) with a free-swinging premental lobe. The hypopharynx is relatively very large and trilobed, the lateral lobes being much larger and densely hairy.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are present on segments three, four and five only, the uniordinal crotchets forming a lateral penellipse.

The anal legs are well developed with a semi-circle of well-developed crotchets anteriorly.

Ornix avellanella Stt.

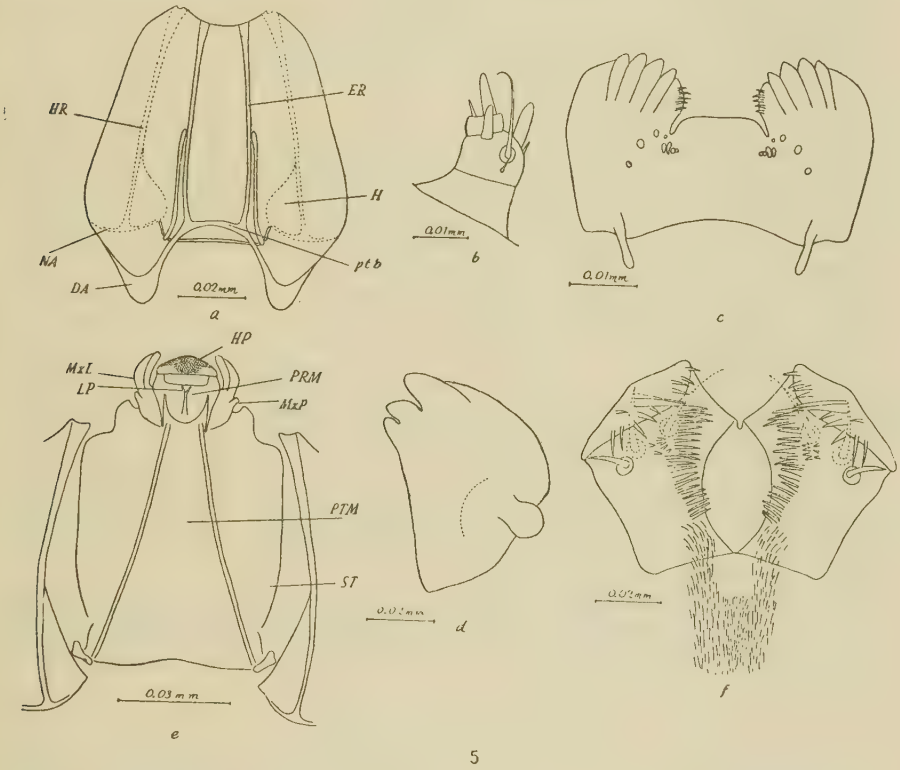
The sap-feeding larva has a flattened body and mines a narrow gallery in the form of a gridiron between two of the principal veins in the epidermis of hazel leaves. This phase lasts for two instars.

The head capsule (fig. 5, a) is very flattened and wedge-shaped. The posterior dorsal prolongations are rather small and pass into the anterior end of the prothorax. The dorsal apodemes (DA) of the postoccipital ridge are

more strongly developed than the ventral (VA). The two arms of the epistomal ridge (ER) diverge very slightly and are connected at their posterior ends by a transverse bar (ptb) of about the same thickness. The hypostomal areas (H) are small and widely separated, while the hypostomal ridges (HR) diverge slightly.

Three ocelli are present, in two groups of two and one respectively, on the margin at the posterior extremity of the head.

The antenna (fig. 5, b) and labrum (fig. 5, c) are specialised and have been described by Trägårdh.



5

Fig. 5.—Sap-feeding stage of *Ornix avellanella* Stt. a, head, dorsal view; b, left antenna, ventral view; c, labrum, ventral view; d, left mandible, ventral view; e, underlip, ventral view. Tissue-feeding stage of *O. avellanella* Stt. f, labrum, ventral view.

The mandible (fig. 5, d) is completely flattened and has four teeth, which are blunt, the third being the largest, while the fourth lies external to and fused with it. The hinge line connecting the dorsal and ventral articulations proceeds directly downwards.

In the underlip the maxillary stipites (fig. 5, e; ST) are very large. The maxillary palpi (MXP) are very small and consist of one segment, while the maxillary lobes (MXL) are very large and flat, consisting of two incurved, spatulate lobes. The premental (PRM) and postmental (PTM) regions are separated by a suture but there is no spinneret. A pair of small hair-like and diverging structures at the anterior end of the prementum possibly represent

labial palpi (LP). The hypopharynx (HP) is more or less rounded and covered with numerous very short hairs and projects in front of the prementum.

There are no thoracic, abdominal or anal legs.

The tissue-feeding larva of *O. avellanella* has a cylindrical body and in the third instar goes over the area of the leaf mined by the sap-feeder. When it has eaten all the tissue between the upper and lower epidermis it leaves the mine to turn down the edge of a leaf and feed therein.

The head capsule is unflattened and of the *Aristotelia* type (p. 66). As the larva is semi-prognathous the head is held at an angle of about 45° to the long axis of the body.

The six ocelli are in the form of a closed ring, the fifth and sixth ventral ocelli having moved backwards to participate in the ring.

The antenna is three-segmented and of the *Aristotelia* type (p. 67), only the basal segment is very large.

The labrum (fig. 5, f) is bilobed with a small median incision anteriorly. The antero-lateral margins are turned down to form flaps with a number of outgrowths, some very large, on their morphological dorsal surface which point inwards. On either side of the epipharyngeal shield is a dense mass of small outgrowths pointing inwards, which are continuous with the relatively long epipharyngeal spines which reach back to the mouth.

There are six teeth in the mandible, of which the first four are dorsal and lie on the same level. The fifth and sixth teeth lie ventral and are smaller than the third and fourth.

The underlip is of the *Aristotelia* type (p. 67) with a free-swinging premental lobe. The hypopharynx has a pair of large, hairy lobes, the maxillulae, with the hairs pointing inwards or backwards.

The thoracic legs are well developed and of the *Aristotelia* type (p. 68).

The abdominal legs are present on segments three, four and five only. The uniordinal crotchets are well developed and form a lateral penellipse enclosing posteriorly a band of larger uniordinal crotchets. This is evidently a reduced multiserial arrangement.

The anal legs are well developed and have a semi-circle of crotchets anteriorly.

O. guttea Hw. differs from *O. avellanella*, in the tissue-feeding stage, in the structure of the labrum only, in which the antero-lateral flaps are wanting.

Phyllocnistis suffusella Zell.

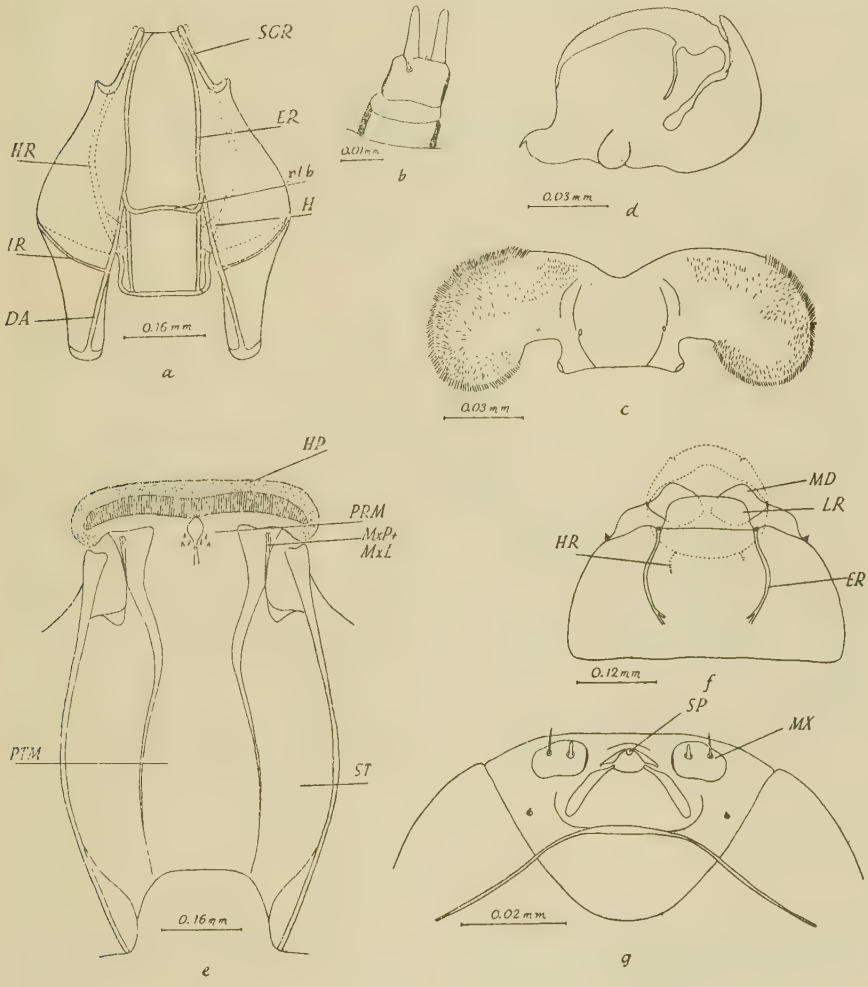
The larva has a flattened body and during the whole of its active feeding life, which lasts for three instars, mines a long tortuous gallery in the upper epidermis of poplar leaves.

The head capsule (fig. 6, a) is flattened and wedge-shaped and has moderately well-developed posterior dorsal prolongations. The two arms of the epistomal ridge (ER) diverge and at the posterior end are connected by a transverse bar (ptb). They then become continuous with the dorsal apodemes (DA) of the postoccipital ridge, which are well developed. A transverse ridge (TR) runs from the lateral margin of the head and connects with the dorsal apodeme of the postoccipital ridge just anterior to the tentorial bridge (TB). The subgenal ridges (SGR) are strongly developed. The hypostomal areas (H) are very small and widely separated, and the hypostomal ridges (HR) converge considerably at the posterior end.

There is a single ocellus placed laterally on the head some distance behind the antenna.

The antenna (fig. 6, b), labrum (fig. 6, c) and mandible (fig. 6, d) are specialised and have been described by Trägårdh.

In the underlip there are no cardines. The maxillary stipites (fig. 6, e; ST) are very large. Maxillary palpi and lobes (MXP and MXL) are possibly



6

FIG. 6.—Sap-feeding stage of *Phyllocnistis suffusella* Zell. a, head, dorsal view; b, left antenna, ventral view; c, labrum, ventral view; d, left mandible, ventral view; e, underlip, ventral view. Prepupal stage of *P. suffusella* Zell. f, head, showing labrum and mandibles, dorsal view; g, mouth-parts, ventral view.

represented by a laterally placed filamentous structure bifurcated at its apical end. Prementum (PRM) and postmentum (PTM) merge into one another and there is no spinneret or labial palpi. The hypopharynx (HP) which is broad and lies anterior to the prementum is laterally expanded and recurved, its surface being covered with innumerable small hairs.

There are no thoracic, abdominal or anal legs. Instead there is a pair of small lateral retractive protuberances on the mesothorax and metathorax and a pair placed laterally on each of the abdominal segments, except the tenth which has none and the eighth which has two pairs.

At the end of the third instar the sap-feeding larva changes to a prepupal form which has a relatively cylindrical body. Its entire activities are concerned with spinning silk to form a small " nidus " by turning down the edge of the leaf.

The head capsule (fig. 6, f) is rather flattened and triangular in shape with the mouth-parts situated in an anterior lobe projecting forwards. Hardly any of the ordinary landmarks are present to establish the homology of the various parts. A pair of inwardly curving ridges, which do not meet, running from the outer extremity of the labrum may represent the two arms of the epistomal ridge (ER), while a pair of short ridges ending blindly may be vestigial hypostomal ridges (HR).

There are no ocelli.

The antenna (fig. 6, f) has one segment only, which is probably the second. It has a pair of small conical sensorial papillae with a longer seta lying between them.

The labrum (fig. 6, f; LR) is a flat, broad plate showing no structure whatsoever.

The mandibles (fig. 6, f; MD) are generally supposed to be absent, but they are undoubtedly present in a vestigial condition. They are present as plates which do not meet in the median line and have only a single articulation, whose exact nature it has been impossible to establish.

The mouth-parts (fig. 6, g) are very specialised and reduced, and it is very difficult to homologise what is present. They are situated in a semi-circular projection at the anterior end of the head capsule. Two relatively large areas placed laterally possibly represent the reduced maxillae (MX). The spinneret (SP) is a rounded, median projection with a large orifice but the presence of labial palpi is doubtful.

There are no thoracic, abdominal or anal legs. A pair of minute lateral protuberances is present on each of segments three to seven of the abdomen.

Lyonetiidae.

Lyonetia clerckella (L.).

The larva has a very flattened body and mines a long, tortuous gallery, venter uppermost, on the upper surface of leaves of apple, hawthorn, birch, etc.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

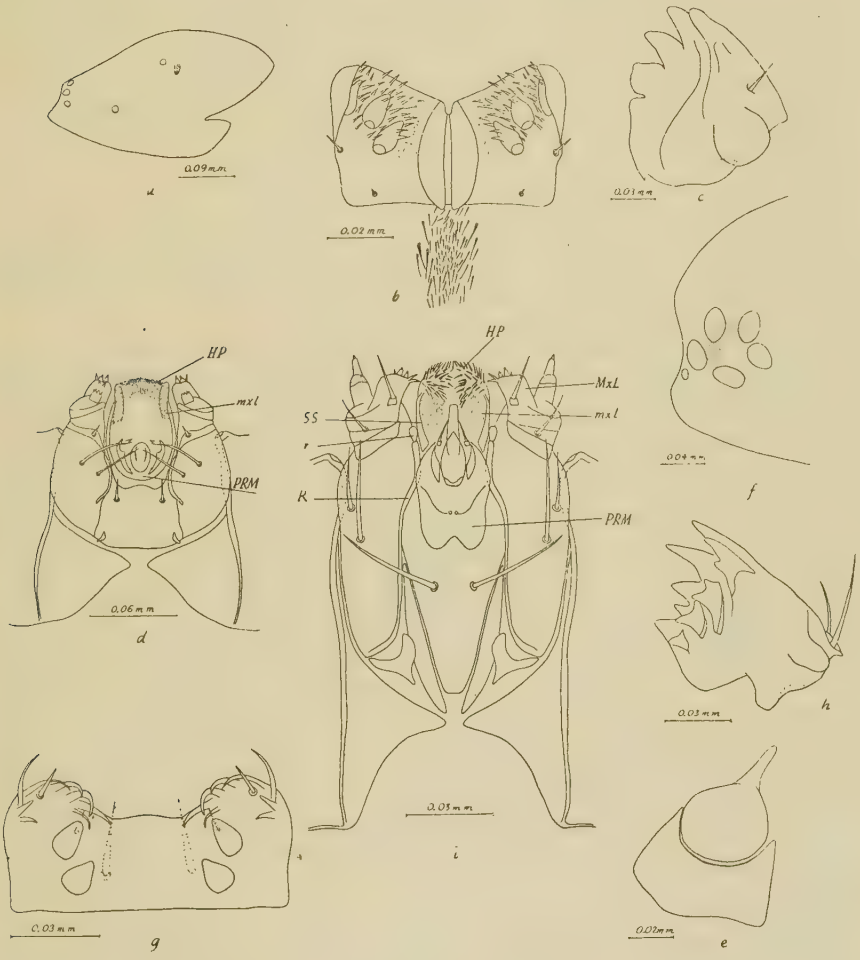
There are six ocelli (fig. 7, a) in two widely separated groups, an anterior and a posterior. The former consists of three ocelli, the third, fourth and sixth. The first and second ocelli comprising the posterior group are placed dorsally at the greatest width of the head, two-thirds of the way back from the anterior extremity of the head. Between the two groups lies the fifth ocellus, which is marginal. Trägårdh includes this latter ocellus in the posterior group.

The antenna is three-segmented and of the *Aristotelia* type (p. 67) but the whole antenna is relatively short.

The labrum (fig. 7, b) is bilobed with a small median incision anteriorly. The antero-lateral margins are turned down to form a pair of small flaps with no outgrowths on them. The anterior half of the labrum is provided with a

large number of small, hair-like outgrowths which are not continuous with the long epipharyngeal spines.

In the mandible (fig. 7, c) a well-defined ridge running from the mesal base to between the fourth and fifth teeth divides it into dorsal and ventral areas,



7

Fig. 7.—*Lyonetia clerckella* (L.). a, ocelli of left side; b, labrum, ventral view; c, left mandible, ventral view; d, underlip, ventral view; e, left mesothoracic leg, ventral view. *Bedellia somnulentella* (Zell.). f, ocelli of left side; g, labrum, ventral view; h, left mandible, ventral view; i, underlip, ventral view.

the former carrying four teeth and the latter two. The first three teeth lie on the same level, while the sixth is vestigial.

In the underlip the premental lobe (fig. 7, d; PRM) has receded considerably and is incapable of being swung in and out. The recession has also carried the spinneret to an extreme posterior position. The anterior part of the underlip is formed of the hypopharynx (HP) alone, which is large, flat and

covered with innumerable small hairs dorsally. It has a pair of small maxillulae (mxl).

The thoracic legs are very small and probably non-functional. They consist of two segments only (fig. 7, e), a relatively broad basal segment with its distal end concave into which fits the more or less circular terminal segment with its claw. In the early stages the legs are absent.

Abdominal legs are absent but their positions on segments three to six are marked by a compact mass of crotchets which occasionally give the impression of forming a uniserial circle. They are absent in early instars.

The anal legs are not distinctly present but there are two rows of crotchets arranged in a semi-circle.

Bedellia somnulentella (Zell.).

The larva has a cylindrical body, and mines in the first instar a narrow gallery on the upper surface of the leaves of *Convolvulus*. Thereafter it mines an open blotch, which it leaves at times to walk at random on a network of silk on the surface of the leaf, or to mine a new blotch.

The head capsule is unflattened and of the *Aristotelia* type (p. 66).

The first five ocelli (fig. 7, f), which are relatively large and partly provided with pigment, either within or without, form a closed ring. The sixth ocellus is much smaller and occupies its normal ventral position.

There are only two segments in the antenna, the basal having disappeared.

The flat median lobe in the trilobed labrum (fig. 7, g) is set lower than the lateral lobes, whose anterior margins are provided with six or seven large ventral outgrowths which are curved inwards. There are no epipharyngeal spines.

The powerful mandible (fig. 7, h) is relatively thick and extends mesally to a considerable extent. There are two rows of teeth, a dorsal row of pointed teeth of varying sizes and a ventral row of four teeth. Three of these are set on broad bases and are conical, while the second and fourth have small accessory teeth. All the teeth appear to be functional.

In the underlip the maxillary lobes (fig. 7, i; MXL) have a pair of rather long, somewhat hook-shaped bristles on the mesal side. The same recession of the premental lobe seen in *L. clerckella* is seen in this species, but not to quite such an extent. The premental lobe (PRM) is incapable of being swung in and out. The hypopharynx (HP) is very hairy and has a pair of finely hairy maxillulae (mxl).

The thoracic legs are well developed and of the *Aristotelia* type (p. 68). Each pair of legs is set rather close together and the trochanter can be made out.

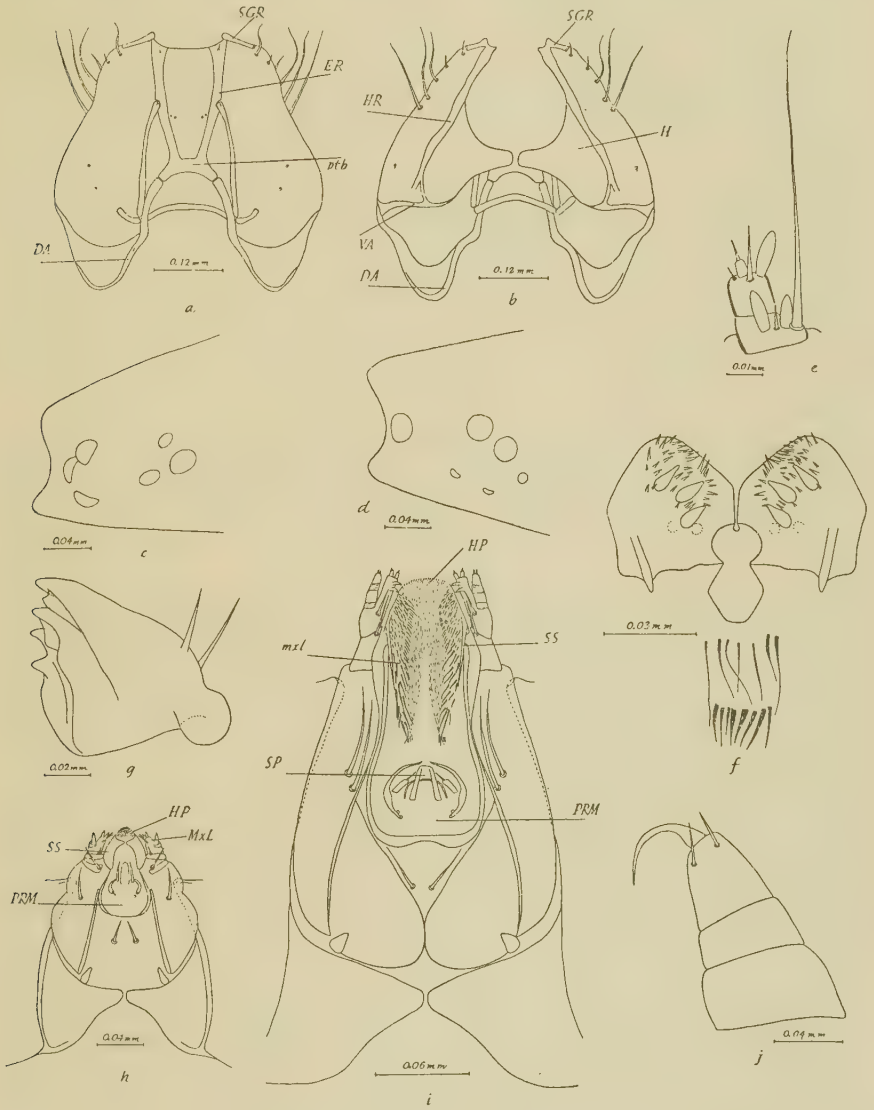
The abdominal legs are present on segments three to six. Those on the third and sixth segments are very small, while those on the fourth and fifth are longer and set close together. All have a uniserial circle of well-developed uniordinal crotchets.

The anal legs are strongly developed and have a semi-circle of crotchets placed anteriorly.

Leucoptera.

The larva of *L. laburnella* Stt. has a cylindrical body and mines a spiral blotch beginning as a very narrow gallery on the upper surface of leaves of laburnum. The larva of *L. scitella* Zell. has a flattened body and mines a circular blotch on the upper surface of leaves of hawthorn and apple. The

larva of *L. lotella* Stt. has a flattened body and mines a circular blotch on the upper surface of leaves of *Lotus*.



8

FIG. 8.—*Leucoptera scitella* Zell. a, head, dorsal view; b, head, ventral view. *L. laburnella* Stt. c, ocelli of left side. *L. scitella* Zell. d, ocelli of left side; e, left antenna, ventral view; f, labrum, ventral view. *L. laburnella* Stt. g, left mandible, ventral view. *L. lotella* Stt. h, underlip, ventral view. *L. scitella* Zell. i, underlip, ventral view. *L. laburnella* Stt. j, left mesothoracic leg, ventral view.

The head capsule (fig. 8, a, b) of this genus is typically flattened and the posterior dorsal prolongations extend half-way into the prothorax. The dorsal apodemes (DA) of the postoccipital ridge are strongly developed especi-

ally at the posterior extremities. The two arms of the epistomal ridge (fig. 8, a; ER) are very strongly developed and converge posteriorly where they are joined by a short, broad, transverse bar (ptb). The subgenal ridges (fig. 8, a, b; SGR) are well developed. The hypostomal areas (fig. 8, b; H) are relatively large but do not show the marked forward extension seen in *Tischeria* and *Nepticula*. The hypostomal ridges (HR) diverge for the greater part of their length but turn inwards slightly at their posterior extremity. In *L. lotella* the posterior dorsal prolongations are relatively smaller than in the other two species.

The ocelli in *L. laburnella* (fig. 8, c) are in two groups, an anterior marginal one, consisting of the third and fourth, and a posterior consisting of the first, second and fifth. The sixth ocellus lies ventral. Trägårdh figures all the ocelli on the dorsal surface, but with this I cannot agree.

In *L. scitella* the most anterior ocellus (fig. 8, d) is the fourth, which is marginal and placed just behind the antenna. The rest are placed, some distance behind, in a flattened ring open forwards, the sixth ocellus having moved backwards considerably. The fifth and sixth ocelli are very small and probably non-functional.

In *L. lotella* the ocelli are in two groups, an anterior and a posterior, separated by a short gap and ranged round a flattened ring. The anterior consists of the third, fourth and sixth ocelli, while the posterior consists of the first, second and fifth. All the ocelli are well developed.

The antenna (fig. 8, e), which has been described by Trägårdh, is two-segmented, the basal segment having disappeared.

The labrum (fig. 8, f) in *L. scitella* and *L. laburnella* has a long median incision extending for two-thirds of the way into the labrum and ending in a round hole. All the ordinary setae are absent. The anterior part of the ventral surface has numerous, moderately stout, outgrowths, some of which project beyond the margin. The epipharyngeal spines are relatively long and extend from the level of the epipharyngeal shield to the region of the mouth. *L. lotella* differs only in having a short median incision.

The mandible of *L. laburnella* (fig. 8, g) is dorso-ventrally flattened and expanded laterally at the same time so that each tooth lies outside and slightly above the level of the next. There are six teeth, four of which are conical and progressively larger, while the other two are vestigial and lie alongside the third and fourth. The hinge line connecting the mandibular articulations proceeds directly downwards. In *L. scitella* and *L. lotella* the vestigial teeth are absent.

In the underlip of *L. lotella* (fig. 8, h) the maxillary lobes (MXL) have a pair of moderately long hook-shaped bristles directed mesad. The relative positions of the hypopharynx (HP) and the premental lobe (PRM) are more or less the same as in *Bedellia somnulentella*. The premental lobe is probably incapable of being swung in and out, as fulcral sclerites are absent. The suspensorial sclerites (SS) of the hypopharynx, which is globular in shape with its apex conical and covered with minute hairs, are strongly developed.

In *L. scitella* the premental lobe (fig. 8, i; PRM) has receded far more than in *L. clerckella*, *B. somnulentella* or *L. lotella*, so that the spinneret is in an extreme posterior position. The lateral thickenings of the premental lobe extend far forwards and the suspensorial sclerites (SS) of the hypopharynx (HP) are supported on them. The hypopharynx, which is cone-shaped with a flat apex, is densely tufted with hairs at its anterior end and carries a pair of long maxillulae (mxl), covered with long hairs posteriorly. The spinneret (SP) is relatively

small but is absent in the earlier instars, all that can be made out being a pair of palp-like structures arising from a common stem.

L. laburnella is essentially similar to *L. scitella* except that the maxillulae are not so markedly evident. In early stages the spinneret is absent and the hairs on the hypopharynx show a scattered arrangement, while the maxillulae cannot be made out.

In *L. lotella* the thoracic legs are four-segmented, small but functional. In *L. laburnella* (fig. 8, j) and *L. scitella* they are small and non-functional. In early stages of *L. scitella* they are present as minute protuberances, but are absent in *L. laburnella*.

The abdominal legs, on segments three to six, in *L. lotella* are small and functional. In *L. laburnella* and *L. scitella* they are very weakly developed and have a uniserial circle of uniordinal crotchets. Abdominal legs are absent in early stages.

The anal legs are small with a few crotchets present in a semi-circle anteriorly.

Tischeriidae.

The larvae belonging to this family are typically flattened. *Tischeria complanella* (Hb.) mines a large whitish blotch on the upper surface of leaves of oak and *T. marginea* (Hw.) a trumpet-shaped blotch beginning as a short gallery on the upper surface of leaves of *Rubus*. The larvae are peculiar in lining the floor of the mine with silk and ejecting their frass through a hole in the lower cuticle.

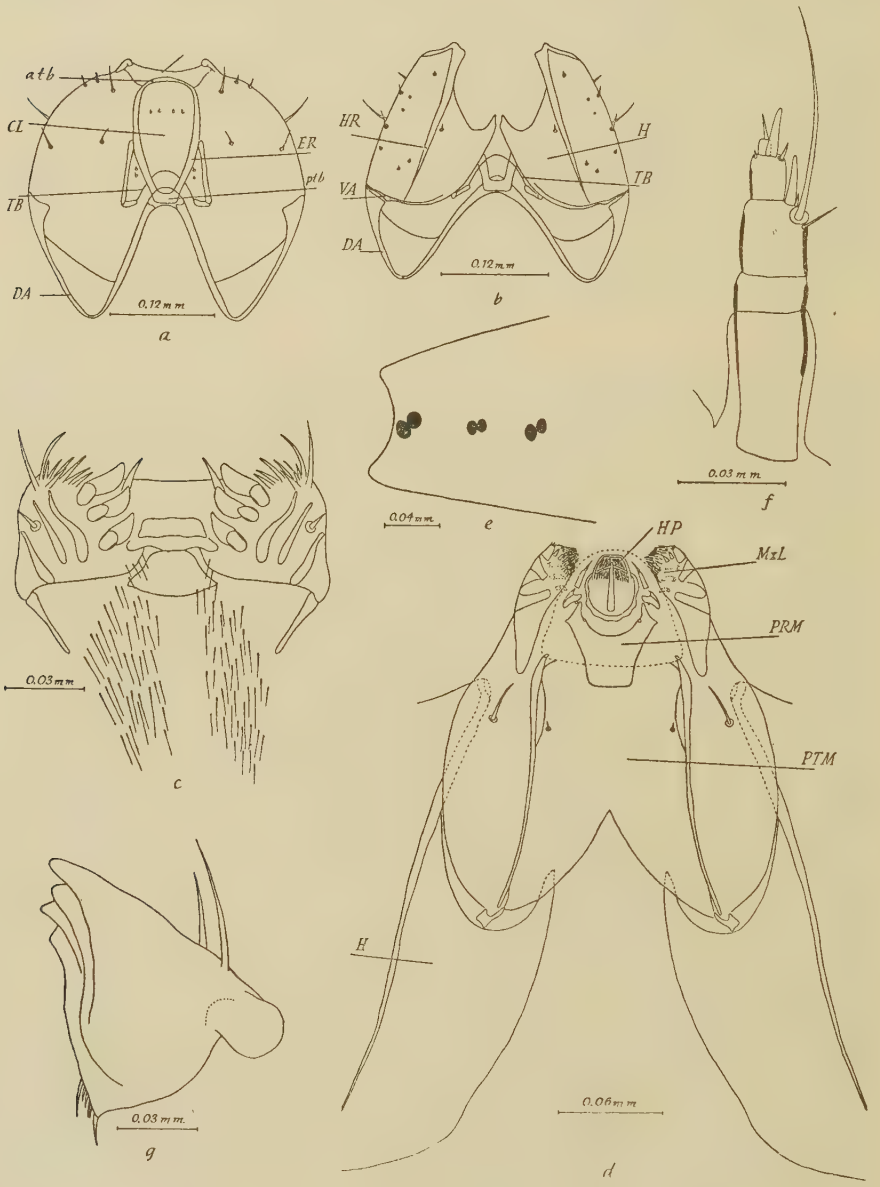
The head capsule (fig. 9, a, b) in both species is very flattened, and the posterior dorsal prolongations extend half-way into the prothorax. The dorsal apodemes (DA) of the postoccipital ridge are very strongly developed at the posterior extremities. The two arms of the epistomal ridge (fig. 9, a; ER) converge but do not meet posteriorly and are connected by a short, thick, transverse bar (ptb) and also anteriorly by a narrow bar (atb) lying against the submarginal thickening (SMR) of the anterior end of the clypeus (CL). The hypostomal areas (fig. 9, b; H) are relatively large and extend forwards for some distance, while the hypostomal ridges (HR) diverge considerably. The tentorial bridge (fig. 9, a, b; TB) is very slender and upwardly arched and has been overlooked by Grandi (1933) in *T. complanella*. This diminution in size of the tentorium is possibly associated with the nature of the premental lobe, which can be swung in and out only to a very limited extent. The muscles associated with this movement are inserted on the tentorial bridge in normal forms. In *Tischeria* it was not possible to make them out.

In both species the six ocelli (fig. 9, e) are placed marginally or submarginally in three groups of two each, the first being just posterior to the antenna. All are heavily pigmented.

In *T. complanella* the basal segment of the antenna (fig. 9, f) is longer than the second and third together and is peculiar in being enclosed by a cylindrical cuticular prolongation of the general surface of the head. When the antenna is fully extended this cuticular covering encloses about four-fifths of the basal segment, but the antenna can be withdrawn so that it encloses this segment as well as the second up to the level of the long seta characteristic of this segment. The antenna of *T. marginea* is similar.

The labrum (fig. 9, c) in both species is trilobed with the median lobe flat. The three pairs of ventral epipharyngeal setae have been modified to form large hook-like structures pointing inwards. At the antero-lateral margins a number

of stout outgrowths project beyond the edge. All ordinary setae are absent on the dorsal surface but two ventral pairs are present. The posterior half of the labrum is rather heavily sclerotised and is further strengthened by the



9

Fig. 9.—*Tischeria marginea* Hw. a, head, dorsal view; b, head, ventral view; c, labrum, ventral view; d, underlip, ventral view (the dotted line represents a sclerotised flap which actually lies ventral to the structures lying within). *T. complanella* (Hb.). e, ocelli of left side; f, left antenna, ventral view; g, left mandible, ventral view.

presence of three pairs of rod-like structures. The epipharyngeal spines are relatively long and extend back to the mouth from the level of the epipharyngeal shield.

The mandible in *T. complanella* (fig. 9, g) is triangular in shape and so completely flattened dorso-ventrally that the four triangular teeth lie one above the other. At the mesal base of the mandible is a fringe of five or six hairs pointing backwards. The hinge line joining the mandibular articulations proceeds directly downwards. *T. marginea* is essentially the same except that the third tooth is small and tends to be obscured.

In the underlip of both species the maxillary palpi (fig. 9, d; MXP), the maxillary lobes (MXL) and the prementa l lobe (PRM) occupy a relatively small area in comparison with the rest of the underlip. The maxillary lobes are, however, relatively very large and flap-like and densely covered with long hairs on the mesal side. On the dorsal surface there are three large hook-like structures directed mesally, which are similar to those present on the ventral surface of the labrum. The whole of the prementa l lobe is covered by a sclerotised flap which appears to be an extension of the postmentum (PTM), but of this one cannot be certain. The hypopharynx (HP) is cone-like with a dense tuft of hairs at its apex, while the suspensorial sclerites are strongly developed. If the prementa l lobe can be swung in and out at all, the movement must be very limited. The spinneret is well developed at all stages.

The thoracic legs in both species are reduced to minute, slightly sclerotised protuberances.

The abdominal legs are absent in *T. complanella*. In *T. marginea* the positions of the legs are marked by the presence of crotchets on segments three to six. They are variable in number and arrangement even on the same segment, and generally consist of one or two transverse bands of small uniordinal crotchets.

In *T. complanella* the anal legs are marked by a diagonal row of well-developed crotchets. In *T. marginea* there are two rows, an anterior and a posterior.

Nepticulidae.

The larvae of *Nepticula* have very flattened bodies and mine either long, tortuous galleries as in *N. angulifasciella* Stt. on *Rubus* or blotches, beginning as galleries, as in *N. salicis* (Fabr.) on *Salix*.

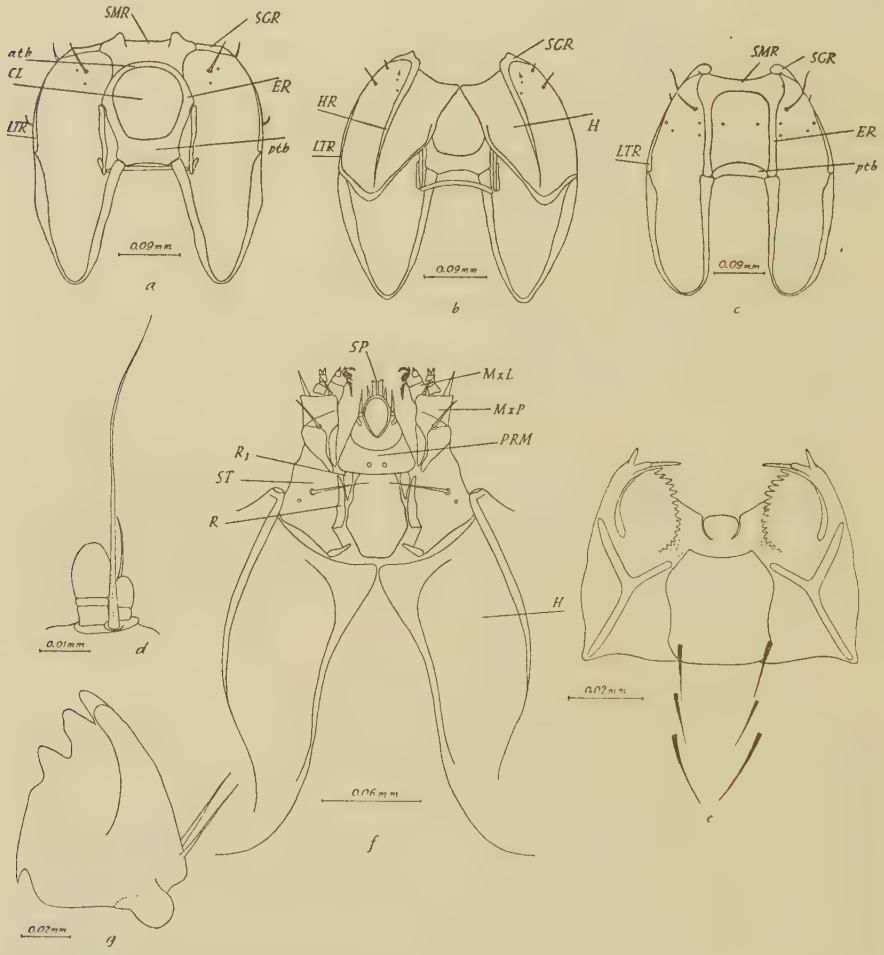
The head capsule of *N. anomalella* Gz. (fig. 10, a, b) is very flattened and the posterior dorsal prolongations, which are about half as long as the rest of the head, extend two-thirds of the way into the prothorax. The two arms of the epistomal ridge (fig. 10, a; ER) are rather semi-circular in shape and are connected posteriorly by a very broad transverse bar (atb), which lies against the submarginal thickening (SMR) of the clypeus (CL). The hypostomal areas (fig. 10, b; H) are relatively very large and extend far forwards, while the hypostomal ridges (HR) diverge. A lateral ridge (fig. 10, a, b; LTR) runs from a point just behind the laterally placed ocellus, which is some distance away from the antenna, to the junction of the dorsal and ventral regions of the head. The subgenal ridges (SGR) are strongly developed.

In *N. salicis*, too, the head capsule (fig. 10, c) is very flattened and the posterior dorsal prolongations lie parallel. The two very broad arms of the epistomal ridge (ER) are also parallel and are connected posteriorly by a stout transverse bar (ptb), which does not appear to be fused to the epistomal ridge. The submarginal thickening (SMR) is broad. A lateral ridge (LTR) is present as in *N. anomalella*, and the subgenal ridges (SGR) are strongly developed.

The head capsules of *N. microtheriella* Stt. and *N. aurella* Stt. have an epistomal ridge similar to that of *N. salicis*.

The genus is characterised by the presence of a single lateral ocellus placed a little distance behind the antenna.

The antenna (fig. 10, d) and the labrum (fig. 10, e) are specialised and have been described by Trägårdh.



10

Fig. 10.—*Nepticula anomalella* (Gz.). a, head, dorsal view; b, head, ventral view. *N. salicis* Fabr. c, head, dorsal view. *N. anomalella* (Gz.). d, left antenna, ventral view; e, labrum, ventral view; f, underlip, ventral view. *N. salicis* (Fabr.). g, left mandible, ventral view.

The mandible (fig. 10, g) has typically only four teeth, the first having become continuous with the mesal edge. The second, third and fourth lie dorsal and are on the same level, while the fifth lies ventral.

In the underlip the forward extension of the hypostomal areas already noted in *Tischeria* has resulted in the underlip complex becoming very dimin-

ished in size, so that the maxillary stipites (fig. 10, f; ST) are only about as long as the maxillary palpi (MXP). Along the mesal margin of each stipes there are two sclerites (R, R_1), the more distal pair possibly acting as the fulcra on which the premental lobe is swung in and out. This movement, however, is probably limited to a very small arc and the fulcra, therefore, are peculiar in being placed at the proximal end of the premental lobe and not laterally. The maxillary lobes (MXL) are three-segmented and carry at their apices a long, inwardly curved spur and a number of hairs in the form of a comb, also inwardly directed, on the second segment. The premental lobe (PRM) is triangular in shape and the spinneret (SP), which is only a little longer than broad in all the species examined, except in *N. microtheriella* where it is relatively long, is placed at the apex. On either side of the spinneret is a pair of bristles which Trägårdh thinks may represent " the lobus externus of the ligula," meaning, presumably, paraglossae. In early stages the spinneret is absent though labial palpi can be made out faintly.

Thoracic, abdominal and anal legs are absent. Instead, there is a pair of relatively large protuberances on the mesothorax and metathorax and on each of the abdominal segments two to seven.

Eriocraniidae.

Eriocrania sangi Wood.

The larva has a cylindrical body and mines a large blotch, beginning as a very narrow gallery, in which all the tissue between the upper and lower cuticles is eaten, in leaves of birch.

The head capsule (fig. 11, a) is unflattened but the posterior dorsal prolongations are greatly developed, more so than in any other unflattened form, and extend about a third of the way into the prothorax. The dorsal apodemes (DA) of the postoccipital ridge are strongly developed, especially at the posterior extremities. The head has a remarkably delicate tentorium (AT, TB, PT) which has been overlooked by Grandi (1933) and possibly also in the closely related genus *Mnemonica* by Busck and Böving (1914). The anterior tentorial arms are peculiar in being attached to small forwardly directly spurs of the epistomal ridge. The reason for this delicate tentorium is obscure.

There is only a single large ocellus placed at the base of the antenna ventrally.

The antenna is three-segmented but the basal segment is generally very difficult to make out.

The labrum (fig. 11, b) is trilobed, the median lobe being small and convex. The ventral surface is covered with numerous very stout outgrowths, some of which project beyond the anterior margin.

The mandible has four teeth, of which the first three are placed on the same level. The fourth lies ventral and is smaller than the third.

In the underlip the basal segment of the maxillary palpus (fig. 11, c; MXP) has at its ventral anterior extremity a number of hairs, which are especially long on the mesal side and project inwards. The second segment has three or four long, tooth-like structures on its ventral aspect, while a large number of inwardly projecting hairs are present on the mesal aspect of the maxillary lobe (MXL). The hypopharynx (fig. 11, d) has well-developed maxillulae provided with long, sometimes bifurcated, hairs projecting inwards.

There are no thoracic, abdominal or anal legs. Instead, there is a pair of dorsal and ventral retractive protuberances on the mesothorax and metathorax.

Mnemonica auricyanea Wals. described by Busck and Böving (1914) does not appear to differ materially from *Eriocrania*.

IV. Discussion.

The sap-feeding larvae of the early stages of the GRACILARIIDAE have a dorso-ventrally flattened body throughout that phase of their lives. Among

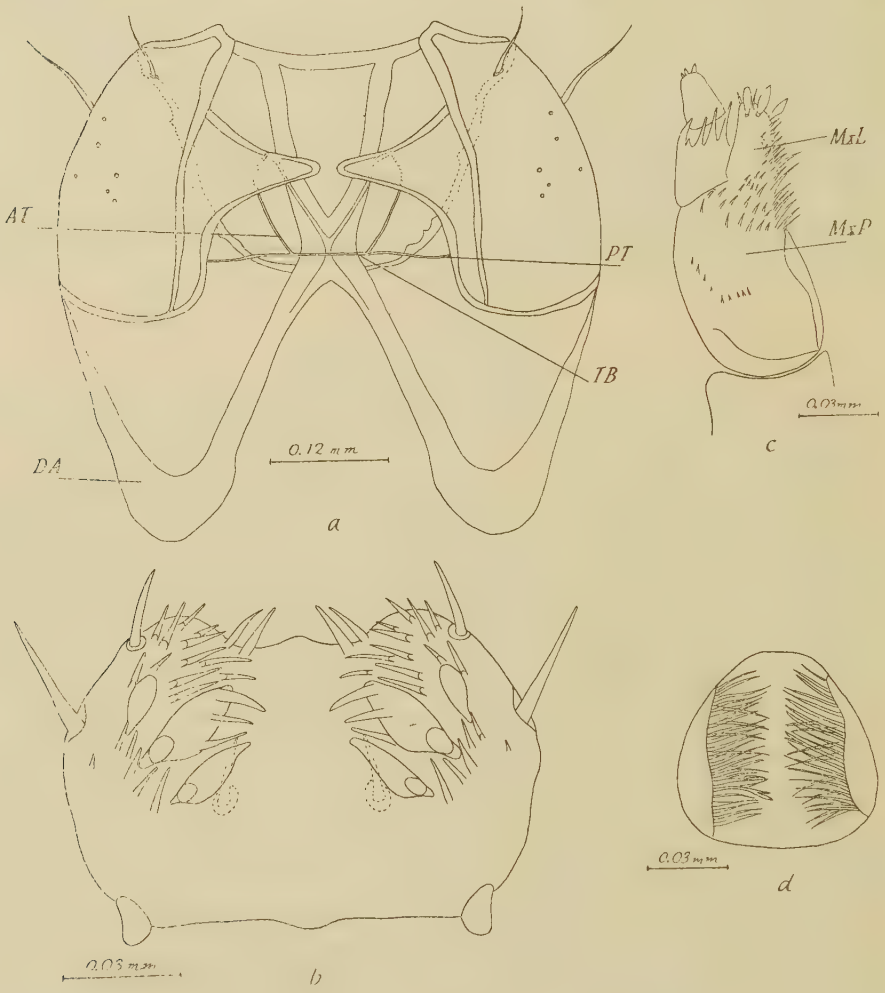


FIG. 11.—*Eriocrania sangi* Wood. a, head, ventral view; b, labrum, ventral view; of maxillary palpus and maxillary lobe, ventral view; d, hypopharynx, dorsal view.

tissue-feeding larvae the flattened body is only occasionally met with, the great majority having an unflattened or cylindrical body. All sap-feeding larvae at a certain moult, which varies in different genera, assume the cylindrical form which is either an active feeding stage as in *Lithocolletis*, *Acrocercops*,

Ornix, *Gracilaria* and *Parectopa* or a passive, non-feeding or prepupal stage as in *Phyllocnistis* and *cameraria*, in which it is relatively cylindrical in appearance, showing that the earlier flattened form is a specialised one.

The habits of the sap-feeder and the type of mine it inhabits show that a flattened head and body are most advantageous to the larva. The larva feeds and extends its mine by shearing the epidermal cells by means of its flattened mandibles, which only work on tissue lying in front of them and not between them as in tissue-feeders. The larva swings the anterior part of its body from side to side in an arc of a circle and thus brings its mandibles into play. This swinging movement is facilitated by the shape of the body, which is widest in the thoracic region, the abdomen tapering rapidly to its end. Each segment of the body is deeply incised, except in *Phyllocnistis*, allowing it to bend in either direction laterally without causing a lateral expansion of the body. In every instance it is only the thin leaf cuticle that separates the larva from the outside world and in its severely restricted mine a flattened head and body is the ideal shape.

However, among tissue-feeding larvae showing a flattened form one cannot attribute the flattening to the type of mine except, possibly, in *Leucoptera scitella*. Here the larva mines a circular blotch in which the cuticle acts as a very tight cover owing to the larva depositing on the underside of it its viscous frass, which on drying hardens the cuticle. The flattening of the head and body is possibly related to the constricted nature of the blotch. *L. lotella* has a very similar mine. But in such flattened forms as *Tischeria* and *Nepticula* the type of mine does not explain the flattening at all.

The majority of tissue-feeding larvae have an unflattened head and a cylindrical body. Such are the larvae of *Coleophora nigricella*, *Plutella maculipennis* and *Incurvaria muscalella* which mine only in the first instar, *Recurvaria nanella* which mines for three instars, the tissue-feeding larvae of the Gracilariidae, some of which such as *Lithocolletis* and *Ornix* superficially resemble external feeders owing to being semi-prognathous, and the specialised larva of *Bedellia somnulentella*. *Eriocrania sangi*, a completely apodal form, has an unflattened head and body but is very specialised in certain respects. Most of the larvae with unflattened heads and cylindrical bodies mine blotches beginning as galleries, with the exception of such forms as *Aristotelia hermanella* and *R. nanella*, which mine galleries throughout. All of them are relatively active in their movements, except *E. sangi*.

The head capsules of leaf-mining larvae fall quite naturally into two groups, the unflattened and the flattened. A description such as " head more or less depressed " for *Lyonetia* used by Fracker is apt to be misleading, as morphologically it has an unflattened head like that of *Aristotelia*.

With the exception of one or two members of the Gracilariidae, which are semi-prognathous, all leaf-mining larvae, whether sap- or tissue-feeding, are prognathous and the head is characterised by the posterior dorsal prolongations, which extend beyond the limit of the ventral surface of the head. This is a character common to all the forms examined, the condition being less pronounced in the unflattened forms. But among flattened tissue-feeding forms, of which there are only four genera, *Tischeria*, *Leucoptera*, *Opostega* and *Nepticula*, this condition is most marked and the posterior dorsal prolongations of the head increase in that order (Trägårdh says that the head of *Elachista* is flattened, but he has not worked out completely its morphology). The highest development of this specialisation is seen in certain species of *Nepticula*, *N. salicis*, for instance, where they are as long as the rest of the head and lie parallel.

Therefore, in general one may say that just as prognathism is a consequence of the leaf-mining habit the relatively greater extent of the posterior dorsal prolongations of the head is a consequence of the flattening among tissue-feeders.

Among sap-feeding larvae, whose heads also display a pronounced flattening, the posterior dorsal prolongations of the head are much less pronounced. This is probably due to the shape of the mandibles, which are flattened blades and used for shearing the epidermis by a side-to-side swing of the head. Relatively much less strain is put on the head and the need for burying the dorsal prolongations in the prothorax to quite such an extent as in tissue-feeders does not exist.

Another characteristic feature among all leaf-miners is that the dorsal apodemes of the postoccipital ridge are more strongly developed than the ventral, which is the reverse of the condition in external feeding forms (see Snodgrass, 1928). They tend in general to be better developed in the flattened forms, whether sap or tissue-feeding.

But the clearest morphological characteristic that differentiates an unflattened from a flattened head lies in the behaviour of the epistomal ridge. In all external feeders it has the form of an inverted V, and all miners with unflattened heads, which are in the majority, show this, while in those larvae with flattened heads the arms do not meet each other at the apex of the V, but lie some distance apart and are connected by a transverse bar. There is also a tendency for the arms of the epistomal ridge to become parallel and this is seen in some species of *Nepticula*, e.g., *N. salicis*, but not in others such as *N. anomalella*, so that it appears that this tendency towards specialisation is either still going on in *Nepticula* or that there are two main lines of evolution.

In the sap-feeders, too, the arms of the epistomal ridge show a similar and in some cases a more pronounced specialisation. In *Parectopa syringella* they are little different from the condition in *Tischeria*, while in *Ornix avellanella* the arms diverge slightly, a tendency which is better developed in *Lithocolletis concomitella* and *Phyllocnistis suffusella*, so much so, that they have become continuous with the dorsal apodemes of the postoccipital ridge with no point of junction between them. A further peculiarity in *L. concomitella* is a short dorsal lateral transverse bar from the posterior extremity of the head which in this species ends blindly but in *P. suffusella* is joined to the combined epistomal ridge and dorsal apodeme of the postoccipital ridge. These larvae feed by swinging their heads from side to side and the ridges have probably been developed as additional struts in the framework of the head to ensure rigidity.

In *Nepticula* there is developed a lateral ridge running from a point just behind the ocellus to the junction of the dorsal and ventral parts of the postoccipital ridge. Such a ridge is described by Heinrich (1918) in *Opostega*, and it probably affords a better attachment for the adductor muscles of the mandibles, as the pronounced flattening of the head has resulted in the virtual disappearance of the genae.

A marked development of the subgenal ridges is characteristic of the flattened head, especially in tissue-feeders. As the mandibles in these forms are powerful structures working in a more or less horizontal plane the ridges probably brace the antero-lateral areas of the head.

The flattening of the head in *Leucoptera*, *Tischeria* and *Nepticula* has resulted in the enlargement and forward extension of the hypostomal areas, the condition in *Leucoptera* being the least pronounced. This has resulted in a shortening of the maxillary stipites in *Nepticula* and *Tischeria*. The forward extension of the hypostoma has reached its climax in *Opostega*, described by

Heinrich, where they have moved to the anterior end of the head so that a thin, transparent " gula " covers the entire mid-ventral region. Among sap-feeders the flattening of the head has had an opposite effect on the hypostomal areas, which are very small and widely separated, the mid-ventral surface being entirely covered by the maxillary stipites and the postmentum of the labium.

The modification in the arrangement of the ocelli in all sap-feeding and certain tissue-feeding larvae such as *Leucoptera*, *Tischeria* and *Nepticula* is correlated with the flattening of the head. Consequently, the ocelli have come to lie on or about the margin due to the virtual disappearance of the genae. Now, while in a number of forms with unflattened heads such as *Incurvaria*, *Recurvaria* and *Aristotelia* the arrangement is little different from that of an external feeder, in others such as *Lithocolletis*, *Parectopa*, *Bedellia*, *Acrocercops*, *Lyonetia* and *Eriocrania* the arrangement is considerably modified, resulting in the enlargement of some of the ocelli with a corresponding diminution in size or even elimination of others. The question arises whether the modification in arrangement of the ocelli in leaf-mining larvae subserves the visual sense, as in a number of species the ocelli appear to be capable of dealing with forward or horizontal vision or both. This is, however, a matter for conjecture and no experiments to this end have been carried out.

The majority of leaf-mining larvae have a three-segmented antenna, which is also characteristic of external feeders. The reduction or addition of segments that are found in certain forms are often correlated with certain specialised features, such as a flattened head and body as in *Leucoptera* and *Nepticula* which have a two- and one-segmented antenna respectively. In *Nepticula* the reduction may be connected with the larval habit of swinging the head and anterior part of the body from side to side in the narrow galleries so many of them mine. In *L. scitella* the larval habit of extending the mine, which is very restricted vertically, by feeding at the edge of the circular blotch may account for the shortened antenna and the general flattening of the head and body as well. *Lyonetia clerckella*, a species that mines a very narrow, winding gallery, has accommodated its antenna to the habit by shortening it instead of reducing any of the segments.

Trägårdh says that the antenna in sap-feeders is less reduced than in tissue-feeders, and that this is due to it being situated in a lateral hollow of the head. This statement is more or less correct as far as the number of segments is concerned, only *Phyllocnistis* showing a two-segmented condition while *Lithocolletis* has a four-segmented antenna. Actually, the antenna of *Parectopa*, *Ornix* and *Phyllocnistis* is relatively small while in *Lithocolletis* it is relatively long, projects outwards and is then curved inwards at the apical end. This dual method of modifying the antenna appears to be related to the mode of feeding already described. In this at abduction the mandibles appear to open out relatively far more than in tissue-feeders, so that unless the antennae were reduced in size they would get in the way. *Parectopa*, *Ornix* and *Phyllocnistis* have done this, but *Lithocolletis* has met the situation by the novel method of projecting its antenna outwards so that it lies just beyond the range of the mandibles. The antennae of these forms cannot be retracted into the head.

Many tissue-feeding larvae have a labrum that is little different from that of an external feeder, with, however, the number of dorsal setae reduced. Such a relatively unmodified labrum is seen in *Recurvaria*, *Incurvaria*, *Coleophora*, *Plutella* and *Aristotelia hermanella*. Modification of the labrum has taken the form of ventral outgrowths restricted to the anterior half which are present in large numbers in *Eriocrania*, *Leucoptera* and *Ornix*. Some forms

such as *Tischeria*, *Lithocolletis*, *Parectopa* and *Ornix* have the epipharyngeal spines developed to a great extent so that they and the ventral outgrowths are more or less continuous. As the ventral surface of the labrum is continuous with the membranous inner lining of the clypeus, these spines reach back to the mouth. This has been confirmed by examining sagittal sections through the head of the larva of *Lithocolletis concomitella*. Some forms such as *Bedellia* and *Eriocrania*, though having well-developed ventral outgrowths, have no epipharyngeal spines. It is difficult to attribute any function to these outgrowths, though it is possible that any excess of sap that has not already been dealt with by the hypopharynx may be passed back to the mouth by way of the epipharyngeal spines when the latter are well developed.

Among sap-feeding larvae epipharyngeal spines are absent, while only *Phyllocnistis* has any ventral outgrowths, where they are present in large numbers and possibly aid in collecting sap. Trägårdh suggests that the labrum of *Lithocolletis* is used like a saw to cut the epidermal cells. It is certainly serrate in appearance and well sclerotised but the modification, if to such an end, seems an unnecessary one as the mandibles appear powerful enough to perform their function. *Ornix*, however, has a very delicate labrum and the teeth seem incapable of being put to such a strain, while Trägårdh was mistaken in attributing such a function to the labrum of *Gracilaria*, which has no teeth. As he suggests, the large, backwardly directed lobes of the labrum in *Phyllocnistis* have probably the further function of covering the mandibles. This is of the utmost importance as the larva is a sap-feeder throughout its feeding life and attains a relatively large size. The cuticle of the upper surface of the poplar leaf, which *P. suffusella* mines, is very delicate and the danger of it being ruptured is a serious one. This has been obviated by developing a labrum large enough to cover the mandibles.

In a hypognathous larva the mandibles are suspended from the lower margins of the cranium by a hinge line sloping downwards posteriorly and are provided with anterior and posterior articulations. As a consequence of the oblique nature of the mandibular axes the points of the jaws tend to turn upward and somewhat posteriorly during adduction. In the prognathous leaf-mining larvae, however, the anterior and posterior articulations have come to lie dorsal and ventral respectively and in the majority of forms the hinge line connecting them proceeds obliquely downwards and inwards.

Trägårdh has suggested " that as a result of the flattening of the head capsule the mandibles also become dorso-ventrally compressed and this has resulted in the upper half of the edge becoming more horizontal and the ventral half curving inwards so as to lie below the lateral margin." This view is based on the assumption that the head capsule of tissue-feeders is typically flattened. That this is quite an erroneous view has already been seen. It is far more probable that the incurved outer margin of the mandible is a condition carried over from hypognathous ancestors. Such a mandible with a convex outer margin is obviously of little use to a prognathous larva, because at adduction the ventral teeth would not meet their fellows. Therefore, every stage in their reduction can be traced with a corresponding increase in the importance of the dorsal half of the mandible. Thus, *Plutella maculipennis* mines only in the first instar and in spite of a pronounced convexity of the outer margin of the mandible, the most ventral tooth is almost atrophied. Of three ventral teeth in *Lithocolletis concomitella* the most ventral tooth is again vestigial. *Acrocercops* and *Lyonetia* have two ventral teeth, of which one is vestigial. In *Mompha* and *Aristotelia* the single ventral tooth is small, while in *Eriocrania* the most

ventral tooth has disappeared. While the most ventral teeth are thus being eliminated a flattening of that part of the mandible carrying the dorsal teeth has caused most or all of the teeth to become placed on the same level. This is seen in all the above forms in varying degrees.

Tischeria and *Leucoptera*, both forms with flattened heads, have the entire mandible flattened dorso-ventrally so that the teeth lie one above the other, thus showing an entirely different type of adaptation. Further, the hinge line connecting the articulations of the mandibles proceeds directly downwards so that the mandibles move in a horizontal plane, unlike other forms where the mandibles move inwards obliquely at adduction. Thus, these two genera have reached the limit of specialisation in this direction, also seen in the sap-feeding stages of the GRACILARIIDAE.

The mandible of *Bedellia* is peculiar in having a complete row of dorsal and ventral teeth, all of which are functional. Whether this is a primitive or specialised condition it is difficult to say.

Among sap-feeders the mandibles are flattened blades used in a manner different from that of tissue-feeders. In the latter the inward movement of the mandibles at adduction enables large pieces of food to be torn off. In sap-feeders the mandibles are effective only if they are kept open, as the teeth can then cause the epidermal cells to be pierced when the head and anterior part of the body are swung from side to side, each mandible working independently of the other.

In the majority of leaf-miners the maxilla is a very conservative structure and the maxillary palpi and lobes are in no way different from those of an external feeder. Their function, as in external feeders, is probably largely tactile. The maxillary palpi carry accessory structures in only a single genus, *Eriocrania*, where three or four long, tooth-like processes are present near its apex ventrally. The maxillary lobes, however, are provided with hairs or hook-like or comb-like processes placed on the mesal side in several forms. These include the innumerable long hairs in *Eriocrania*, the combs in *Nepticula anomalella* and the hook-like processes in *Bedellia* and *Leucoptera*. These structures may possibly aid in pushing in any food that may not have found its way into the mouth.

In external feeders the premental lobe and the hypopharynx form a large, projecting composite structure, which is the anterior median lobe of the underlip. At or about the anterior edge of the premental lobe the spinneret is situated and the whole of this composite structure, which in part constitutes the spinning apparatus, can be swung in and out by reductor and productor muscles. The same condition prevails in the majority of leaf-miners, with the exception that the hypopharynx is, in general, densely covered with long or short hairs. A hypopharynx covered with hairs is not peculiar to leaf-miners but the condition has been carried to such an extreme in so many forms that it has not unlikely been induced as an adaptation to the mining habit. The function of such a hypopharynx is probably to mop up the sap that is liberated into the mine, and the free-swinging of the premental lobe enables it to be swept into the direction of the mouth. It is worthy of note that *Eriocrania* has long, occasionally bifurcated, filamentous appendages on its hypopharynx and this larva mines in the very early spring when the plant cells are turgid.

The spinneret in *Aristotelia hermanella*, *A. stipella*, *Coleophora nigricella* and *Incurvaria muscalella* is relatively ill-developed in the first instar but assumes the normal form later. This is particularly noticeable in *C. nigricella* and *I. muscalella*, which mine only in the first instar. They undergo their first moult in the mine and then proceed to cut out a case from it, the sides of which are

glued together with silk. In the second instar of these species the spinneret is well developed. In *Leucoptera* and *Nepticula* no spinneret is present in the first instar but it appears later. Thus, it is evident that there is a tendency for the spinneret to be reduced or absent in stages during which silk is not required and this is probably an adaptation to the mining habit. In forms where silk is spun throughout larval life, as in *Lithocolletis* (in the tissue-feeding stage only), *Tischeria* and *Recurvaria*, the spinneret is always well developed.

The position of the spinneret when it attains its full development in forms where the premental lobe can be swung in and out, is always at or about the tip of the lobe. Trägårdh says that in *Eriocrania* it is placed just behind the tip and shows the earliest stage in the recession of the spinneret in forms he studied. Actually, there does not appear to be anything unusual in the position of the spinneret in the species he figures, nor in two species of the same genus I have examined. Trägårdh's suggestion appears to be mistaken.

It is characteristic of the underlip in most leaf-mining larvae that it is flattened. The advantage of such a flattened underlip to a prognathous larva is obvious. In the forms discussed above this flattening has not resulted in any deviation from the pattern found in external feeders. But in *Bedellia somnulentella*, *Leucoptera lotella*, *Lyonetia clerckella*, *Leucoptera scitella* and *L. laburnella* the flattening of the underlip has gone hand in hand with a marked specialisation of the premental lobe. In these forms it has receded to a greater or lesser extent, leaving the hypopharynx to form the anterior part of the underlip. The recession of the premental lobe is more marked in *L. clerckella*, *L. scitella* and *L. laburnella* than in *B. somnulentella* and *L. lotella*. Thus in certain species of *Leucoptera* this recession is still going on or there are two lines of evolution. *L. lotella* resembles somewhat *Proleucoptera albella* Cham. described by Heinrich (1918).

Now most leaf-mining larvae do not need to spin silk in the mine so that it is quite understandable that an organ useless for the greater part of larval activity should be subordinated to one of fundamental importance. Correlated with the recession of the premental lobe is the inability for it to be swung in and out freely as in other forms. The recession in *Bedellia*, with its long well-developed spinneret, is inexplicable as the larva mines an open blotch, which it leaves at frequent intervals, to walk upon a network of silk it spins on the surface of the leaf. In *Tischeria* the whole of the premental lobe is covered by a sclerotised flap. While this would afford a smooth surface to the underlip, its presence in a genus that lines the floor of the mine with silk is peculiar.

Trägårdh says that in *Nepticula* the spinneret itself is modified to form the underlip. This statement is not supported by a study of his own figures or by preparations of a number of species examined by me. The spinneret is generally broad and flat but relatively small. The underlip itself is excessively flattened.

The mouth-parts of the sap-feeding larvae exhibit a very high degree of specialisation. In them the general flattening of the head and body has made the larva perfectly adapted for a life in the vertically restricted space of the mine, which is in the epidermis of the leaf. Correlated with this the underlip is excessively flattened and all projecting structures such as maxillary palpi and lobes and labial palpi have also been reduced and flattened or eliminated, while the spinneret is absent in all forms as the larva spins no silk in this stage. The mandibles and hypopharynx are, however, well developed and all other structures have been subordinated to them. This is probably because of the peculiar mode of feeding already referred to, by which the liberated sap is collected by the prominent, hairy hypopharynx. As all other structures are

useless for this purpose, they have been progressively eliminated and the very flattened smooth underlip has been evolved to facilitate the lateral movements of the anterior part of the body.

The larvae of the leaf-mining Lepidoptera can be divided into two classes, the active and the sluggish, in relation to their movements in the mine. The former are provided with well-developed thoracic legs, which are similar to those of an external feeder, while the latter show legs in varying degrees of reduction. For instance, while in *Leucoptera* and *Lyonetia* very small legs are present which are probably non-functional, *Tischeria* has merely minute protuberances and in *Eriocrania* and *Antispila* they are completely absent. In *Eriocrania* a pair of dorsal and ventral retractile protuberances on the mesothorax and metathorax have taken the place of legs, while non-retractile ventral protuberances are present on the same segments in *Nepticula*. The presence or absence of functional legs cannot be attributed to the type of mine the larva inhabits, except in *Lyonetia clerckella*, where the reduction in size of the legs is probably correlated with the fact that the larva's progression forwards, in its very narrow gallery, is limited entirely by the rate at which it feeds. Further, it is peculiar in mining venter uppermost. In general, one may say that irrespective of the type of mine, reduction or loss of the thoracic legs is often associated with a flattened body or a flattened head or both and the specialisation of the mouth-parts already discussed, especially recession of the prementa l lobe. But all larvae with well-developed thoracic legs have cylindrical bodies with unflattened heads and a normal prementa l lobe.

In general active larvae with well-developed thoracic legs tend to have well-developed abdominal and anal legs. *Mompha*, which mines venter uppermost, is an exception. Also, *Coleophora nigricella* and *Incurvaria muscalella*, where the larvae mine in the first instar only and are case-bearers subsequently.

The tissue-feeding larvae of the Gracilariidae are characterised by the absence of abdominal legs on the sixth segment. Fracker (1915) points out that, where reduction has taken place as in certain Noctuidae, Nolidae and Geometridae, it is always the pair on the third segment that has disappeared.

Abdominal legs, like the thoracic, tend to be reduced or lost in sluggish larvae. Crotchets in these forms are rarely present in large numbers and when they are, as in *Leucoptera* and *Lyonetia*, they are in a very ineffective condition. Sometimes the abdominal legs are absent as in *Tischeria marginea* but their positions are marked by the presence of crotchets. In *T. complanella* and *Eriocrania*, however, both abdominal legs and crotchets are absent. In *Nepticula*, instead of abdominal legs, there is developed a pair of protuberances on each of the segments two to seven, similar in appearance to those present on the thorax. It is difficult to say whether this is a primitive or specialised condition.

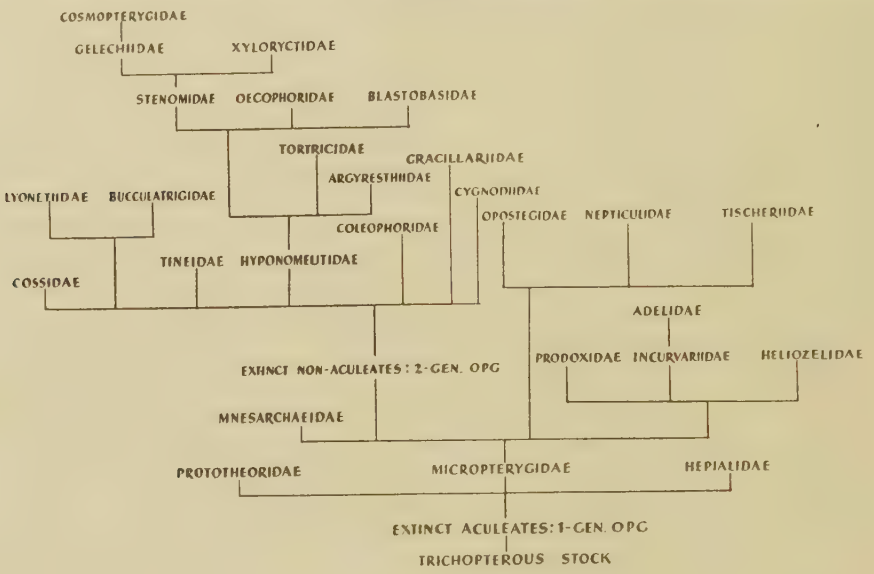
Among sap-feeders thoracic and abdominal legs are absent, except for minute protuberances in *Lithocolletis* and lateral, retractile protuberances in *Phyllocnistis*. Sap-feeders, by the nature of their lives, are very sluggish and the absence of thoracic and abdominal legs is understandable. The lateral protuberances in *Phyllocnistis* are so placed that they could be of no aid in locomotion and are possibly tactile.

V. The Leaf-Mining Habit in Relation to the Phylogeny of the Microlepidoptera.

The most important classifications of the Microlepidoptera are those of Busck (1914) and Meyrick (1928), based on wing venation, and that of Busck (1931),

based on the structure of the female genitalia (fig. 12) and, of these, the classifications of Busck are the more satisfactory.

Certain adult Lepidoptera are characterised by the presence of minute, hollow outgrowths of the general surface of the wing called aculei, which correspond to the microtrichia of other insects. The presence of aculei in a few families of Lepidoptera is, therefore, a primitive character of fundamental importance which has not been utilised by Meyrick. His phylum " Tineina," which contains most of the leaf-mining families, includes both aculeate and non-aculeate forms and he has also created a special phylum for the aculeate family Nepticulidae. In Busck's classification certain leaf-mining families are clearly demarcated from the rest by the presence of aculei and other vena-



12

Fig. 12.—Phylogeny of the principal families of the Microlepidoptera (After Busck, 1914 and 1931).

tional characteristics. These are the Incurvariidae (the Lamproniadae of Meyrick), Adelidae, Opostegidae, Tischeriidae and Nepticulidae. Meyrick, in addition to creating a phylum for the Nepticulidae, places *Tischeria* and *Opostega* in the Lyonetiidae, a non-aculeate family. In Busck's later work two additions were made to this group, the Eriocraniidae and Heliozelidae.

On a study of the female genitalia, Busck (1931) found that the primitive Jugatae had a single female genital opening at the end of the abdomen placed just below the anus and serving for both copulation and oviposition. The ovipositor in the Hepialidae, Micropterygidae and Mnesarchaeidae is a soft, bilobed structure and the terminal segments of the abdomen are soft and retractable, while in the Eriocraniidae the ovipositor is modified into a strong, piercing instrument, the abdomen being strongly sclerotised.

Among the Frenatae with a single genital opening there are two main groups,

one with a soft ovipositor, including the OPOSTEGIDAE, TISCHERIIDAE and NEPTICULIDAE and descended, presumably, from Micropterygid stock and the other with a piercing ovipositor including the INCURVARIIDAE, HELIOZELIDAE and ADELIDAE and descended, presumably, from Eriocranid stock. The rest of the Frenatae have complex female genitalia with separate apertures for copulation and oviposition. Thus, all the families, whether Jugate or Frenate, with a single genital opening in the female are aculeate.

It is surprising that only four leaf-mining families have developed piercing ovipositors, as oviposition within the leaf would appear to be an advantage. The leaf-mining habit in these four families, which are aculeate and with the female having a single genital opening, is probably not of equal antiquity. For instance, *Eriocrania* and *Mnemonica* (ERIOCRANIIDAE) and *Antispila* (HELIOZELIDAE) are genera which have apodal larvae, an obviously specialised condition that must have taken a very long time to evolve. On the other hand, in the INCURVARIIDAE and ADELIDAE the habit must be of comparatively recent origin as it is confined to the first instar only.

The females of all the other families of leaf-miners have retained the ancient habit of ovipositing on the surface of leaves. One adaptation to the mining habit shown by larvae of most families is that they mine directly into the leaf on hatching, leaving part of the egg shell to act as a lid. The importance of this is obvious. Not only does it do away with the risk of being attacked by a predator but it also keeps the mine free from fungi. Exceptions to this habit must be regarded as being less specialised and the larvae have probably taken to the mining habit more recently. In these cases the larvae hatch out of the egg on the open side and crawl on the surface of the leaf for a time before mining into the leaf, leaving the entrance open. *Plutella maculipennis*, which mines only in the first instar, and *Recurvaria nanella*, which mines for three instars, are examples. The genus *Coleophora* shows both types, although a miner only in the first instar. Thus, in *Coleophora* the mining habit is now becoming more firmly fixed in certain species or there are two main lines of evolution. When the entrance to the mine is left open, as in the above forms, one is inclined to believe that the larva has not mined directly from the egg. The COSMOPTERYGIDAE shows both types as *Cosmopteryx* mines direct, while *Mompha* has an open mine. These examples belong to the higher groups.

The larvae of *Phthorimaea*, *Cosmopteryx* and *Scythris* according to Needham, Frost, and Tothill (1928), *Aristotelia* and *Bedellia* leave their mines, either when the food supply is exhausted or at random, to enter other leaves. This habit is obviously a primitive one and could only be displayed by larvae that have not become completely adapted to the leaf-mining habit. All these larvae, except *Bedellia*, belong to the higher groups. In *Phthorimaea* the habit is so unstable that the same larva may mine in leaves, roots, or stems or feed between spun leaves. Larvae that are well adapted to the mining habit such as *Eriocrania*, *Nepticula* and *Tischeria* are quite incapable of mining into leaves once they have been removed from the mines.

The type of mine may be taken as an indication of the antiquity of the leaf-mining habit. A linear gallery is regarded as being more primitive than a blotch, because the latter almost invariably begins as a gallery. Table I, which has been compiled from Meyrick (1928), summarises the number of leaf-mining and non-leaf-mining genera and species in the leaf-mining and related families in Britain. Also, the number of linear and blotch miners in each genus. It is evident that both linear and blotch miners are distributed at random in most of the families, thus giving the impression that the leaf-mining habit has

TABLE I.—LEAF-MINING AND RELATED FAMILIES OF THE MICROLEPIDOPTERA IN BRITAIN. (Compiled from Meyrick, 1928.)

Family	No. of genera	No. of non-leaf-mining genera	No. of leaf-mining genera	Name of genus	No. of species	No. of leaf-mining species	Linear mines	Blotch mines	No. of non-leaf-mining species	Habits unknown
†HEPIALIDAE	—	—	—	—	—	—	—	—	—	—
†MICROPTERYGIDAE	—	—	—	—	—	—	—	—	—	—
‡ERIOCRANIIDAE	2	—	2	*Eriocrania*	7	7	—	7	—	—
				Mnemonica	2	2	—	2	—	—
‡LAMPRONIIDAE	3	—	3	*Phylloporia*	1	1	—	1	—	—
				**Incurvaria*	2	2	—	2	—	—
				**Lampronia*	8	2	?	?	6	—
HELIOZELIDAE	2	1	1	*Antispila*	2	2	—	2	—	—
ADELIDAE	3	—	3	**Nematois*	5	2	?	?	3	—
				**Adela*	5	2	?	?	3	—
				**Nemophora*	4	2	?	?	—	2
‡NEPTICULIDAE	3	1	2	*Nepticula*	67	66	46	19	1	—
				Trifurcula	3	1	?	?	2	—
†OPOSTEGIDAE	1	1	—	—	—	—	—	—	—	—
‡TISCHERIIDAE	1	—	1	*Tischeria*	5	5	—	5	—	—
‡GRACILARIIDAE	6	—	6	*Lithocolletis*	49	47	—	47	2	—
				Phyllocnistis	2	2	2	—	—	—
				Acrocercops	3	3	—	3	—	—
				**Ornix*	9	9	—	9	—	—
				**Parectopa*	1	1	—	1	—	—
				**Gracilaria*	13	13	?	1	—	—
HYPONOMEUTIDAE	11	5	6	*Ocnerostoma*	1	1	1	—	—	—
				Cedestis	2	1	—	1	1	—
				Argyresthia	24	2	?	?	22	—
				Atemelia	1	1	—	1	—	—
				**Prays*	1	1	?	?	—	—
				**Roesslerstammia*	2	1	?	?	—	1
‡COLEOPHORIDAE	3	2	1	**Coleophora*	51	51	?	1	—	—
†TINEIDAE	15	15	—	—	—	—	—	—	—	—
BUCCULATRIGIDAE	1	—	1	**Bucculatrix*	11	11	1	—	—	—
‡LYONETIIDAE	4	1	3	*Leucoptera*	11	7	—	7	4	—
				Lyonetia	3	2	2	—	1	—
				Bedellia	1	1	—	1	—	—
‡PLUTELLIDAE	5	3	2	**Plutella*	5	1	—	1	4	—
				Acrolepia	3	3	—	3	—	—
EPERMENIIDAE	3	2	1	**Epermenia*	4	2	?	?	2	—
SCYTHRIDAE	1	—	1	*Scythris*	8	1	?	?	7	—
†DOUGLASIIDAE	1	1	—	—	—	—	—	—	—	—
ELACHISTIDAE	3	—	3	*Perittia*	1	1	—	1	—	—
				Stephensia	1	1	—	1	—	—
				Elachista	36	34	33	1	—	2
†GLYPHIPTERYGIDAE	3	3	—	—	—	—	—	—	—	—
†HELIODINIDAE	5	5	—	—	—	—	—	—	—	—
†AEGERIIDAE	3	3	—	—	—	—	—	—	—	—
ORNEODINIDAE	1	—	1	*Orneodes*	1	1	?	?	—	—
OECOPHORIDAE	19	18	1	*Depressaria*	40	1	—	1	38	1
†BLASTOBASIDAE	2	2	—	—	—	—	—	—	—	—
‡GELECHIIDAE	31	28	3	*Aristotelia*	16	3	2	1	7	6
				**Recurvaria*	2	1	1	—	1	—
				Phthorimaea	20	6	?	3	11	3
‡COSMOPTERYGIDAE	5	2	3	*Cosmopteryx*	4	4	1	3	—	—
				Limnoecia	2	1	—	1	1	—
				Mompha	13	6	—	6	6	1

* Leaf-mining for only a part of larval life. † Wholly non-leaf-mining families.
‡ Families dealt with in the present paper.

arisen many times in the course of evolution. This is clearly seen in Busck's phylogenetic tree (fig. 12), where a large number of leaf-mining families occupy the terminal branches, showing that the habit has come to a dead end.

Among tissue-feeders specialisation is most marked in *Lyonetia*, *Bedellia* and *Leucoptera* (LYONETIIDAE), *Tischeria* (TISCHERIIDAE), *Opostega* (OPOSTEGIDAE), *Nepticula* (NEPTICULIDAE), *Eriocrania* (ERIOCRANIIDAE) and possibly *Elachista* (ELACHISTIDAE), about which little is known. Four of these families are aculeate. With the exception of *Bedellia* and *Eriocrania* they comprise forms that have both head and body flattened but they do not necessarily show a specialisation of the same structures to the same degree. However, all of them have a modified arrangement of the ocelli. Some, such as *Tischeria* and *Lyonetia*, have a three-segmented antenna, *Leucoptera* and *Bedellia* a two-segmented and *Nepticula* a one-segmented antenna. The labrum in all is very specialised. *Lyonetia*, *Leucoptera* and *Bedellia* show a recession of the premental lobe, with the hypopharynx forming the anterior part of the underlip. Only in *Eriocrania* is the premental lobe free-swinging, the movement being possibly very limited in *Tischeria* and *Nepticula*. All of them, except *Bedellia*, are relatively sluggish in their movements. The leaf-mining habit is, therefore, of great antiquity in these forms, for the modifications must have taken a long time to evolve.

Heinrich (1918) has attempted to show that the TISCHERIIDAE, NEPTICULIDAE, OPOSTEGIDAE and LEUCOPTERYGIDAE (*Leucoptera* is placed in the LYONETIIDAE by Meyrick) are derived from a common stock, the latter branching off from the Nepticulid stem at a very early date, as their larvae, according to him, show very close affinities. His main argument is the nature of the hypostomal areas in these families. In *Tischeria* and *Nepticula* they display a forward extension which is carried, according to Heinrich, to its climax in *Opostega*, where they occupy an extreme anterior position with the formation of a " gula " posteriorly. Further, he says, this extension of the hypostomal areas in the LEUCOPTERYGIDAE " has distorted a normally proportioned stipes which has not accommodated itself to the change and forced it to slop over the anterior margin of the epicranium and a large part of the area occupied by the postmentum." Now, while the hypostomal areas in *Proleucoptera albella* Cham., which Heinrich figures, show a slight forward extension, in the three species of *Leucoptera* I have examined it is much less marked and do not bear any resemblance to the same structures in *Tischeria* and *Nepticula*. Also, the stipes in *P. albella* and in the species I have examined shows nothing unusual, Heinrich having mistaken a large sclerotised area of the postmentum for a part of the stipes. This is strange, as he figures the mesal thickening which demarcates the inner limit of the stipes.

Other features that show, according to him, the larval affinities of these forms are the lateral ridges in the head of *Opostega* and *Nepticula*, the posterior dorsal prolongations of the head and the divergence of the hypostomal ridges. However, while admitting that the wing aculei in *P. albella* are absent, he suggests that this is not a matter of great importance. This view, that the larval characteristics of these forms show a very close phylogenetic affinity, is not upheld by the work of Busck on the female genitalia of Microlepidoptera. In this he shows that while the TISCHERIIDAE, OPOSTEGIDAE and NEPTICULIDAE, all aculeate families, have a single female genital opening for both copulation and oviposition, and therefore have probably arisen from a common stock, in the LEUCOPTERYGIDAE the female has a complex genital system with separate apertures for copulation and oviposition. This difference, in conjunction with the more important absence of aculei in the LEUCOPTERYGIDAE, shows that the

larvae of these four families display a certain convergence which does not imply a close affinity between the LEUCOPTERYGIDAE and the rest.

Meyrick places *Leucoptera* in the LYONETIIDAE, and with the other larvae of this family it has one peculiarity in common, that is, the premental lobe is recessed to a greater or lesser extent, leaving the hypopharynx to form the anterior median part of the underlip. This recession is confined to the larvae of the LYONETIIDAE alone, and correlated with it is the inability for the premental lobe to be swung in and out as in less specialised forms. In *Leucoptera* either this recession is still going on or there are two lines of evolution, for in *L. lotella* the premental lobe has receded to a much less extent than in *L. scitella* or *L. laburnella*. Further, it has small functional thoracic and abdominal legs which in the latter two species are non-functional.

The GRACILARIIDAE, comprising the genera *Lithocolletis*, *Ornix*, *Phyllocnistis*, *Gracilaria*, *Parectopa* and *Acrocercops*, is a very compact group of cosmopolitan distribution and numbering among them more leaf-mining species than all the rest. The chief feature that characterises these genera is the sap-feeding habit of the early larval stages. *Ornix*, *Gracilaria* and *Parectopa* have two such instars, *Lithocolletis* and *Acrocercops* three, while *Phyllocnistis* is a sap-feeder throughout its feeding life lasting for three instars. The " Flat-Larval " or *Cameraria* group of *Lithocolletis*, found only in North America, has five such instars. At a single moult the sap-feeding larvae, in all except *Phyllocnistis* and *Cameraria*, revert to the normal active tissue-feeding type. In *Phyllocnistis* the larva of the fourth instar reverts to the cylindrical form, which is a non-feeding or prepupal stage whose sole function is that of spinning the cocoon. *Cameraria* has two prepupal instars.

The question arises—are the sap- and tissue-feeding larvae hypermetamorphic? Imms (1934) defines hypermetamorphism as follows: " When an insect in its development passes through two or more markedly different larval instars it is said to undergo hypermetamorphism. This phase is accompanied as a rule by a marked change in larval life." According to this definition there can be no doubt that the sap- and tissue-feeding instars of the GRACILARIIDAE are hypermetamorphic. The sap-feeding larva is very specialised and its head and body are very flattened, the mouth-parts reduced considerably, the spinneret being absent, and the mandibles being converted into flattened blades, while the hypopharynx is greatly enlarged and covered with hairs, which enable it to collect the sap. In *Lithocolletis*, *Acrocercops*, *Ornix*, *Gracilaria* and *Parectopa* at a certain moult the larva reverts to the active tissue-feeding type with a cylindrical body. But in *Cameraria* and *Phyllocnistis* this latter stage is inactive and only concerned with spinning the cocoon.

The hypermetamorphism shown by the GRACILARIIDAE is not of the usual type as seen in the MELOIDAE, for instance, where in the first instar an active, hard-skinned, campodeiform larva called a triungulin after seeking its host changes into a soft-bodied eruciform larva which in turn passes into a pseudopupal or coarctate condition. The GRACILARIIDAE show the reverse of this and a sluggish, very specialised larva reverts later to an active more normal type. It is evident that *Cameraria* and *Phyllocnistis* have reached the limit of specialisation by eliminating an active larva.

Twenty-one of the twenty-eight British families of Microlepidoptera listed in Table I have taken to the leaf-mining habit. The table shows that the habit has become better fixed in the lower families than the higher. This is reflected in the higher percentage of mining than non-mining genera and species in the lower families.

VI. Summary.

Principal features exhibited by the majority of leaf-mining Lepidopterous larvae.

1. The body is unflattened and cylindrical.
2. The head capsule is unflattened and has typically a pair of posterior dorsal prolongations which extend beyond the limit of the ventral surface of the head. The dorsal apodemes of the postoccipital ridge are better developed than the ventral.
3. The arrangement of the ocelli in some forms with an unflattened head is rather similar to that of an external feeder, but in others it is specialised and some of the ocelli may be well developed while others may be reduced or even eliminated.
4. The antenna is three-segmented.
5. The labrum is unspecialised, except for a reduction in the number of dorsal setae, in a number of forms. In others ventral outgrowths in conjunction with the epipharyngeal spines possibly form an accessory mode of collecting sap.
6. In all forms there is a tendency for the ventral teeth of the mandible to be reduced or vestigial with an increasing importance of the dorsal teeth, which tend to be placed on the same level.
7. In the majority of forms the maxilla is unspecialised. In a few such as *Leucoptera*, *Eriocrania* and *Nepticula*, hook-like, hair-like or comb-like structures are present which possibly help in pushing food in towards the mouth.
8. In all unspecialised forms the premental lobe can be swung in and out freely.
9. The spinneret tends to be ill developed or absent in early stages of those larvae that do not spin silk in the mine.
10. The hypopharynx always tends to be well developed and hairy and is instrumental in collecting sap.
11. Thoracic, abdominal and anal legs are well developed in larvae that are active in their movements but tend to be reduced or absent in sluggish forms.

Principal features exhibited by sap-feeding larvae.

12. The body is always very flattened, the segments being deeply incised, except in *Phyllocnistis*.
13. The head is always very flattened but the posterior dorsal prolongations are not so markedly evident as in tissue-feeders with a flattened head. The two arms of the epistomal ridge do not meet posteriorly but are joined by a transverse bar. The hypostomal areas are small and widely separated, except in *Lithocolletis*.
14. The ocelli are always placed marginally due to the pronounced flattening of the head.
15. The antenna is either relatively short as in *Ornix*, *Parectopa* and *Phyllocnistis* or relatively long and projected outwards as in *Lithocolletis*. Both types of arrangement have probably been induced by the peculiar mode of feeding and the position of the mandibles at adduction.
16. The labrum is very large and probably prevents the mandible from rupturing the roof of the mine in *Phyllocnistis*. It also possibly acts as an accessory mode of collecting sap.

17. The mandibles are horizontal blades in which the hinge line connecting the dorsal and ventral articulations proceeds directly downwards. They are effective only when kept fully open, and cut the epidermal cells lying in front of them as the larva swings its head and anterior part of the body from side to side.
18. The maxillary palpi and lobes are reduced or absent, while the stipites are greatly developed.
19. The spinneret is always absent, while labial palpi are possibly represented, even as vestiges, only in *Ornix* and *Lithocolletis*.
20. The hypopharynx is well developed, hairy, projects in front of the prementum and is modified for collecting sap.
21. Thoracic, abdominal and anal legs are absent.

The main tendencies observable in tissue-feeding leaf-mining larvae with increasing specialisation.

22. The body is flattened as in *Lyonetia*, *Leucoptera*, *Tischeria* and *Nepticula*.
23. The head is flattened with the posterior dorsal prolongations more pronounced than in unflattened forms. The two arms of the epistomal ridge do not meet posteriorly but are joined by a transverse bar. The hypostomal areas in *Tischeria* and *Nepticula* show a marked forward extension.
24. The ocelli in forms with a flattened head are placed on or about the margin due to the virtual disappearance of the genae.
25. The antenna in *Leucoptera*, *Bedellia* and *Nepticula* shows a reduced number of segments.
26. In *Leucoptera* and *Tischeria* the hinge line connecting the dorsal and ventral articulations of the mandible, which is flattened dorso-ventrally, proceeds directly downwards.
27. In the LYONETIIDAE the premental lobe, which cannot be swung in and out, has receded to a greater or lesser extent, leaving the hypopharynx alone to form the anterior part of the underlip.
28. Thoracic, abdominal and anal legs show an increasing reduction in flattened forms, which are sluggish in their movements. Structures analogous to reduced legs are present in *Nepticula*.

VII. References.

BRAUN, A. F., 1909, Phylogeny of the Lithocolletid group (Prelim. Survey). *Canad. Ent.* **41** : 419–423, 1 fig.

BUSCK, A., 1914, On the classification of the Microlepidoptera. *Proc. ent. Soc. Wash.* **16** : 46–54.

——, 1931, On the female genitalia of the Microlepidoptera and their importance in classification and determination of these moths. *Bull. Brooklyn ent. Soc.* **26** : 199–211, 5 pls.

BUSCK, A., and BÖVING, A. G., 1914, On *Mnemonica auricyanea* Walsingham. *Proc. ent. Soc. Wash.* **16** : 151–163, 8 pls.

CHAMBERS, V. T., 1879, Annual address, *J. Cincinn. Soc. nat. Hist.* **2** : 71–92, 1 pl.

CHAPMAN, T. A., 1902, A classification of *Gracilaria* and allied genera. *Entomologist* **35** : 81, 138, 159.

DAS, G. M., 1937, The musculature of the mouth parts of insect larvae. *Quart. J. micr. Sci.* **80** : 39–80, 12 pls.

DE GRYSE, J. J., 1915, Some modifications in the hypopharynx in lepidopterous larvae. *Proc. ent. Soc. Wash.* **17** : 173–178, 3 pls.

DIMMOCK, G., 1880, The trophi and chitinous supports in *Gracilaria*. *Psyche*, **3** : 99–103, 4 figs.

FOLSOM, J. W., 1909, *Entomology*. Philadelphia.

FRACKER, S. B., 1915, Classification of lepidopterous larvae. *Illinois biol. Monogr.* **2** : 1–161, 10 pls.

GRANDI, G., 1933, Morfologia ed etologia comparata di Insetti a regime specializzatto. IV. La morfologia comparata di vari stati larvali di 30 Microlepidotteri minatori appartenenti a 15 generi ed a 11 famiglie. *Boll. Lab. Ent. Bologna* **5** : 143–307, 129 fig.

HEINRICH, C., 1918, On the lepidopterous genus *Opostega* and its larval affinities. *Proc. ent. Soc. Wash.* **20** : 27–34, 4 pls.

HEINRICH, C., and DE GRYSE, J. J., 1915, On *Acrocercops strigifinitella* Clemens. *Proc. ent. Soc. Wash.* **17** : 6–14, 9 pls.

HERING, M., 1935–37, *Die Blatt-Minen Mittel- und Nord-Europas einschliesslich Englands*. Neubrandenburg.

IMMS, A. D., 1934, *Textbook of Entomology*, 3rd ed. London.

MEYRICK, E., 1928, *Revised Handbook of British Lepidoptera*. London.

NEEDHAM, J. G., FROST, S. W., and TOTHILL, B. H., 1928, *Leaf Mining Insects*. London.

SNODGRASS, R. E., 1928, The morphology and evolution of the insect head and its appendages. *Smithson. misc. Coll.* **81** : 1–158, 57 figs.

TRÄGÅRDH, I., 1913, Contributions towards the comparative morphology of the trophi of the lepidopterous leaf miners. *Ark. Zool.* **8** : 1–49, 67 figs.

TUTT, J. W., 1899, *British Lepidoptera* **1**. London.

VIII. List of Abbreviations Used.

AC, accessory plate of cardo or submaxillary sclerite; AT, anterior tentorial arm; atb, anterior transverse bar; C, cardo; CL, clypeus; Cx, coxa; DA, dorsal apodeme of postoccipital ridge; ER, epistomal ridge; ES, epipharyngeal seta; ESH, epipharyngeal shield; ESP, epipharyngeal cuticular spines; F, frons; Fe, femur; H, hypostomal area; HP, hypopharynx; HR, hypostomal ridge; LP, labial palpus; LTR, lateral ridge of head; MD, mandible; MX, maxilla; MXL, maxillary lobe; mxl, maxillula; MXP, maxillary palpus; PG, postgena; PRM, prementum; PT, posterior tentorial arm; Pt, pretarsus; ptb, posterior transverse bar; PTM, postmentum; R, mesal thickening of stipes; R_1 anterior mesal thickening of stipes; r, fulcral sclerite; SGR, subgenal ridge; SMR, submarginal thickening; SP, spinneret; SS, suspensorial sclerite of hypopharynx; ST, stipes; T, torma; Ta, tarsus; TB, tentorial bridge; Tb, tibia; TR, transverse ridge of head; VA, ventral apodeme of postoccipital ridge.

IX. Index to Species Described.

Acrocercops brongniardella, 74
Aristotelia hermanella, 65
Aristotelia stipella, 68
Bedellia somnulentella, 82
**Coleophora nigricella*, 71
Eriocrania sangi, 89
**Incurvaria muscalella*, 71
Leucoptera laburnella, 82
Leucoptera lotella, 83
Leucoptera scitella, 82
Lithocolletis concomitella, 72
Lithocolletis coryli, 72
Lyonetia clerckella, 80
Mompha sp., 70
Nepticula angulifasciella, 87
Nepticula anomalella, 87
Nepticula aurella, 88
Nepticula microtheriella, 88
Nepticula salicis, 88
**Ornix avellanella*, 76
**Ornix guttea*, 78
**Parectopa syringella*, 74
Phyllocnistis suffusella, 78
**Plutella maculipennis*, 70
**Recurvaria nanella*, 68
Tischeria complanella, 85
Tischeria marginea, 85

* Leaf-miners for only a part of larval life.